Colony Dynamics of Heron Communities: Ecological and Historical Perspectives

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Abstract

Colonial nesting occurs in most avian species, especially in waterbirds. For colonial breeding birds, the presence and persistence of suitable breeding colony sites are important factors for the maintenance of bird populations. Long-term studies of colonial herons and egrets are well conducted in Europe and the USA, but not in East and South-East Asia. In this study, I investigated colony dynamics of herons and egrets based on 51-years data around Ibaraki Prefecture, Japan.

In Chapter 1, I address the 10-year colony dynamics from 2002 to 2011. Although the local populations of herons and egrets in the study area persisted, variations in colony sizes and species composition ratios increased. The population dynamics differed among the six constituent species: while *Ardea alba* (Great Egret) and *Nycticorax nycticorax* (Black-crowned Night Heron) remained relatively constant, *A. cinerea* (Grey Heron) and *Egretta intermedia* (Intermediate Egret) increased, and *E. garzetta* (Little Egret) and *Bubulcus coromandus* (Eastern Cattle Egret) decreased. The marked increase of the *A. cinerea* population during the decade contributed to the increasing temporal variation in colony size and in species composition ratio.

In Chapter 2, I clarify the spacing mechanisms underlying the distribution of colony sites. I evaluated the repulsive force against each colony site from all surrounding colony sites by summing up their inter-colony distance considering the inverse-square law of physics. Most colony sites maintained consistent distances each other, and new colony sites experienced stronger repulsive forces than did reused colony sites. New colony sites that were established in locations distant from neighboring colony sites persisted for longer periods of time. These results suggest that colonies exhibit a preference for relocating to sites with low repulsive forces ay the same or nearby locations as in previous years.

In Chapter 3, I examine whether heron colonies exhibit site fidelity despite herons being facultative reusers of previously occupied colony locations. Since some colonies shifted to nearby locations when their former sites were destroyed, their site fidelity was

analyzed by applying the correlated random walk. Results revealed that 41 out of 61 colonies (67%), that were formed in the study area from 1963 to 2013, exhibited site fidelity. A high rate of site fidelity at the colony level may originate from a few faithful pioneer individuals with many others following them.

In Chapter 4, in order to clarify whether the presence of pioneers played a role in facilitating the establishment of new colonies as well as persistence of colonies, I analyze the pioneer/follower relationship among the constituent species of mixed-species colonies by considering *A. cinerea* as a pioneer. I hypothesized that two ecological features of *A. cinerea*, solitariness and early nesting habits, may facilitate the establishment and persistence of mixed-species colonies. Using 16-year data including periods both before (1997-2004) and after (2005-2012) the expansion of *A. cinerea*, I found that after the *A. cinerea* expansion, more than half of colony establishments were pioneered by *A. cinerea*, and the number of abandonments decreased. Colonies with *A. cinerea* had a greater propensity to persist, whereas those that had never included *A. cinerea* were prone to being abandoned. These results suggest that *A. cinerea* began to take the initiative in establishing colonies, and other heron species began to follow them in colony site selection.

This study illustrates that mixed-species heron colonies are distributed in such a way that inter-colony distance is maintained while exhibiting a preference for relocating to the same or nearby sites as in previous years. Despite the fact that the constituent individuals of a colony are likely to be replaced frequently, colonies tend to persist. Focusing on pioneer/follower relationships would be helpful to reveal the decision making process of gregarious animals. Historical as well as ecological perspective is essential to understanding the dynamics of animal communities.

Key-words

breeding site selection, egret, follower, long-term census, pioneer, population dynamics, site fidelity

General Introduction

A bird colony is a large congregation of individuals of one or more species of bird that nest or roost in proximity at a particular location. Colonial nesting occurs in most avian groups (Lack 1968; Brown et al. 1990; Rolland et al. 1998), includes most species of seabirds (Danchin and Wagner 1997) (such as auks, terns, gulls and albatrosses), wetland species (such as herons, egrets and storks), and a few passerines (such as weaverbirds and swallows). Colonial nesting is the least understood of all avian breeding systems (Brown and Brown 2001), but it may be an evolutionary response to a shortage of safe nesting sites and abundance or unpredictable food sources which are far away from the nest sites (Rolland et al. 1998). The study of coloniality may have much to tell us about the ecology and evolution of group-living animals (Brown and Brown 2001).

Herons and egrets (Ardeidae) are large birds commonly found in aquatic habitats worldwide (Kushlan and Hafner 2000). Despite most species of colonial birds such as seabirds and swallows form colonies on the same cliffs or islands for many years because of the limitation of available breeding sites (Lack 1968), herons and egrets form colonies on comparatively unrestricted resources such as trees, bushes, reeds and the ground (Kushlan and Hancock 2005). Many previous studies therefore have been conducted using heron colonies in terms of the relationships between size and distribution of colonies and surrounding environmental factors (Fasola 1983; Gibbs et al. 1987; Fasola and Alieri 1992; Hafner and Fasola 1997; Tourenq et al. 2000; Tourenq et al. 2004; Fasola et al. 2010). Monitoring programs, especially when long-term, help to assess population fluctuations associated with environmental changes or management actions (Kushlan 1979). Long-term monitoring studies on nesting populations of colonial herons and egrets are well documented in Europe (e.g., Stafford 1971; Tourenq et al. 2000; Fasola et al. 2010), Australia (McKilligan 2001), and the USA (Kelly et al. 2007). In East and Southeast Asia, however, long-term records for breeding populations of colonial nesting herons and egrets only exist in Hong Kong and Vietnam (Kushlan and Hafner 2000; Wong and Young 2006). Lack of local information makes it difficult to

assess the current status of these birds.

In Japan, there are six Ardeidae species of colonial herons and egrets: *Ardea cinerea* (Grey Heron), *A. alba* (Great Egret), *Egretta intermedia* (Intermediate Egret), *E. garzetta* (Little Egret), *Bubulcus coromandus* (Eastern Cattle Egret), and *Nycticorax nycticorax* (Black-crowned Night Heron). Every spring to summer, tens of thousands of pairs nest close to one another on trees or bamboo thickets usually in mixed-species colonies. Previous studies have suggested that the population of herons and egrets in Japan has been decreasing (Narusue 1992; Sasaki 2001). For instance, in the Noda area of Saitama Prefecture, located in the northern suburbs of Tokyo in the Kanto Plain, there had been one of the largest and oldest colony in Japan. It began in the 1710s in the Edo era (1603 - 1867), and there were 20,000-40,000 individual herons and egrets at its peak from the 1910s to the 1950s. Since the 1960s, however, industry in Japan has greatly developed, and the habitats of the herons and egrets have changed drastically. The Noda colony disappeared in 1972, and similarly, both the population and the average colony size of these species declined in the Kanto Plain (Narusue 1992). *E. intermedia* populations had been especially declining, and it is now categorized as a near-threatened species on the revised Red Data Book of Japan (Ministry of the Environment 2002).

The Environmental Agency of Japan (1994) showed that in Ibaraki prefecture, in the eastern part of the Kanto Plain, both the average colony size and the population of *E. intermedia* were large compared to elsewhere in Japan, and this suggests that data from this area could provide important information for future assessment of populations of colonial breeding herons and egrets in Japan and other parts of Asia. In this region, distribution of colonies has been researched by members of the Population Ecology Laboratory since 1983, and those data were first compiled by Koshida (2007). From 1999 to 2000, colony censuses with aerial photographic counts using aircraft were carried out by Fujioka et al. (2001). Tohyama (2005) modified the methods for aerial surveys, and censuses using a small radio-controlled paraglider have been carried out by members

of the Population Ecology Laboratory since 2002. I took over the colony censuses from 2008. In addition, I collected literature from local amateur avian researchers to minimize missing information for colonies especially during periods in which surveys by the Laboratory members were not intensive. I compiled colony data around Ibaraki Prefecture from both local literature and laboratory data. The compiled data consequently includes colonies from 1963 to 2013 (Fig. 1).

From these 51 years of data for colonies around Ibaraki Prefecture, I investigated the colony dynamics of herons and egrets from ecological and historical perspectives. For colonial breeding species, the presence and persistence of suitable breeding colony sites are important factors for the maintenance of the population. In the following four chapters, I describe a series of analyses of colony dynamics. Chapters 1 and 2 provide a basis for understanding the heron communities in the study area. In Chapter 1, I summarize the results of the 10-year colony censuses from 2002 to 2011 to show changes in the number, sizes and species composition ratios of colonies and the population size of each species. In Chapter 2, I analyze the spacing mechanisms underlying the distribution of colonies using repulsive force. I found that colony sites established in locations distant from neighboring colony sites persisted for a longer period of time. In Chapter 3, I examine whether colonies exhibit a preference for relocating to the same or nearby sites as in previous years. I demonstrate that heron colonies exhibit site fidelity despite being facultative reusers of previously occupied colony locations. In Chapter 4, I ask whether the presence of pioneer species played a role in facilitating the establishment and persistence of colonies. I reveal the pioneer/follower relationship among the constituent species of mixed-species colonies focusing on the recent expansion of *A. cinerea* as an incorporation of the pioneer.

This study illustrates that mixed-species heron colonies are distributed in such a way that inter-colony distance is maintained while exhibiting a preference for relocating to the same or nearby sites as in previous years. Despite the fact that the constituent individuals of a colony are likely to be replaced frequently, colonies tend to persist.

Collective philopatry, or facultative site fidelity at the colony level, may originate from a few faithful pioneer individuals with many others following them. It is highly likely that pioneer/follower relationships underlie the decision making process of gregarious animals, as I observed in heron communities. Historical as well as ecological perspective is essential to understanding the dynamics of animal communities.

Chapter 1

Increasing Variation in Population Size and Species Composition Ratio in Mixed-species Heron Colonies in Japan

1.1 Introduction

Herons and egrets (Ardeidae) are commonly found in aquatic habitats worldwide (Kushlan and Hafner 2000). In Europe, long-term population trends of such species have been well investigated, and some factors that explain how and why their population sizes fluctuate at regional level have been revealed: cold winters (Stafford 1971; Reynolds 1979; Hafner and Fasola 1997; Fasola et al. 2010), rainfall (McKilligan 2001), water levels (Grull and Ranner 1998), habitat conditions (Tourenq et al. 2000; Tourenq et al. 2004), aquaculture (Fleury and Sherry 1995), and human disturbance (Fasola et al. 2010). In East and South-East Asia, long-term records of breeding populations of colonial nesting herons and egrets only exist in Hong Kong and Vietnam (Kushlan and Hafner 2000; Wong and Young 2006). Lack of local information makes it difficult to assess the current status of these birds.

In Japan, Grey Heron *Ardea cinerea*, Great Egret *A. alba*, Intermediate Egret *Egretta intermedia*, Little Egret *E. garzetta*, Cattle Egret *Bubulcus coromandus*, and Black-crowned Night Heron *Nycticorax nycticorax* breed in mixed-species colonies. Nationwide research was carried out in 1980 and 1992 (Research Division of the Wild

Bird Society of Japan 1981; Environmental Agency of Japan 1994), and it was reported that single- and mixed-species colonies were distributed throughout Japan's lowlands. Although there are many observations of colonies in various areas, long-term local populations have only been reported by Narusue (1992) and Matsunaga et al. (2000).

Narusue (1992) argued that both the population and the average colony size of these species declined from the 1940s to 1992 in Saitama Prefecture, west Kanto Plain, due to loss of foraging areas and use of agricultural chemicals. Change in the irrigation of rice fields from shallow earth ditches to deep concrete-walled channels and the decline in aquatic prey caused in the decline of Intermediate Egret (Narusue and Uchida 1993; Lane and Fujioka 1998), the commonest egret until the 1960s, but now categorized as 'near threatened' (Ministry of the Environment 2002). In contrast, a long-term study of Grey Herons in Hokkaido by Matsunaga et al. (2000) reported an increase in population and the number of colonies. There are currently no other reliable data to assess population trends of herons and egrets in Japan.

Environmental Agency of Japan (1994) showed that in Ibaraki Prefecture, east Kanto, Japan, both the average colony size and the population of Intermediate Egret were large compared to elsewhere in Japan, and this suggested that data from this area could provide important information for future assessment of populations of colonial breeding herons and egrets in Japan and other parts of Asia. In this study, colony censuses were carried out from 2002 to 2011 in Ibaraki Prefecture, to investigate trends in these populations using a combination of aerial and ground surveys. The changes are discussed here with reference to the trends in population dynamics of each species, changes in the nesting vegetation and the number of consecutive years that colonies existed.

1.2 Methods

Study area

The present study focused on Ibaraki Prefecture and parts of Tochigi and Chiba Prefectures in Honshu, central Japan (35°47'N - 36°46'N, 139°46'E - 140°41'E, Fig. 2). The area is in the east Kanto Plain, near Lake Kasumigaura, and includes six major rivers: Kuji, Naka, Sakura, Kokai, Kinu, and Tone. The north is mountainous, but the predominant land use in other areas is farming, with large areas along the rivers being used for rice production. There are also lotus fields near Lake Kasumigaura, areas of lowland forests and human habitations. Japan started a national project to consolidate rice production in 1963; this included extending irrigation ditches, improving service roads, and enlarging fields to facilitate mechanised farming equipment. It was largely complete by 1980 (Himiyama and Kikuchi 2007), but conducted in part of the study area into the last decade, being 78% completed by 2010 in Ibaraki Prefecture (http://www.nouson.pref.ibaraki.jp/). The climate of the region is moderate with an annual average air temperature of 14.0 ± 0.1 °C and an annual precipitation of 1,388.2 ± 54.3 mm. Despite a small annual decrease in rice cultivation, neither climate nor land use showed obvious changes during the study period (Fig. 3).

The herons and egrets breed from March to August, but there is considerable variation from species to species (Fig. 4). The Grey Heron arrives first in March, Great Egret, Little Egret, and Black-crowned Night Heron arrive in April; these species are residents and wanderers, and some individuals winter in this area. Finally, the migrant species arrive, Intermediate Egret in late April and Cattle Egret by early May (A. Abe *in litt.* 2006). Usually Black-crowned Night Heron is nocturnal, but during the breeding season it is also active during the day.

Colonies were located in bamboo thickets, trees or a mixture of both. Bamboo thickets were composed of Moso Bamboo *Phyllostachys pubescens*, Simon Bamboo *Pleioblastus simonii*, or Dwarf Bamboo *Pl. chino*. There were two types of trees: conifers and broadleaf trees. Conifer tree sites consisted mainly of Japanese Red Pine *Pinus densiflora*, Japanese Cedar *Cryptomeria japonica* and Japanese Cypress *Chamaecyparis obtusa*; broadleaf tree sites were mainly Japanese Zelkova *Zelkova*

serrata, Japanese Oak *Quercus serrata* and Yoshino Cherry *Prunus* × *yedoensis*.

Censuses of colonies

Every year from 2002 to 2011, ground-based searches of colony locations were conducted referring to the locations of the colonies in previous year; between March and early May, 93 ± 0.02 SE% of the colony sites in year t were found by checking the places where colonies had been located in year t-1. When a colony was abandoned, checks were made to determine whether other colonies had formed nearby. Local literature and personal communication were used to locate colonies that had not been found during the authors' own field work. Site vegetation was recorded by identifying bamboo or tree species holding at least one nest.

In small colonies that had fewer than approximately 50 nests, if all nests were visible from outside or within the site, the nests of each species were counted directly from the ground, and the breeding populations estimated by doubling the number of nests counted. In most cases, ground-based counting were impossible due to large colony size, the impenetrable nature of dense bamboo thickets or other vegetation such as tall trees. Hence, counts were made using a combination of aerial and ground surveys, following the method of Fujioka et al. (2001).

For aerial surveys, a small 'Sky Surfer' radio-controlled paraglider was used (Green Corporation, Japan, Fig. 5a). This equipment is quieter than fixed-wing aircraft or helicopters commonly used for bird colony censuses (Kushlan 1979; Rodgers et al. 2005), and very suitable in this case where more than 80% of the colonies were close to residential areas. Aerial photographs of each colony were taken at an altitude of 30-50 m above the ground just before sunrise (approximately 04h00), when most birds were in the colony. Photography was started in mid-May after arrival of Cattle Egrets, and was continued until early July when distinguishing between growing nestlings and adults became difficult (Fig. 4). Aerial photographs were taken once during that period at each site. All individuals of the four light-colored species Great Egret, Intermediate Egret,

Little Egret, and Cattle Egret in the images were counted (Fig. 5b). For large colonies, several photographs were used to obtain a complete composite image of the colony.

Because it was not feasible to identify the light-colored species only using the photographs, and because the two dark-colored species Grey Heron and Black-crowned Night Heron were difficult to count in the photographs, species composition ratios —the proportion of each species within a colony— were estimated using data from ground surveys. The number of individuals of all species going in and out of each colony for a period of 30 minutes in the daytime were counted using binoculars. It was very difficult to identify to species level white egrets flying in and out at the same time, observation only focused on the common range, approximately a 30-degree field of vision. In the case of large colonies, surveys were carried out from two or three different directions. Ground surveys were made once or twice in June, the peak chick-rearing period (Fig. 4), when all species engage in frequent foraging flights. Thirty minutes is much shorter than the typical duration of one foraging flight and it was assumed that each individual counted, whether arriving or departing was observed only once during the observation period and therefore the observed proportion of each species reflects the species composition ratio of the colony.

The total estimated number of individuals in the colony (T = colony size), was calculated using $T = \frac{A}{1-x}$, where A is the actual number of light-colored individuals counted from aerial photographs, and x is the sum of the proportion of Grey Herons and Black-crowned Night Herons obtained from the ground survey. The estimated population size of each species in the colony was obtained by multiplying the colony size by the proportion of each species.

Data analyses

To determine the number of colonies each year, the number of observed colony sites was first counted. But the number of sites itself was not taken to be the number of colonies because a few colony sites were very close to each other despite foraging ranges having

radii of about 10 km, and sometimes over 20 km (Nabeya 2011). An earlier study showed that heron colonies are evenly distributed to avoid overlap of foraging sites (Gibbs et al. 1987). Consequently if colony sites were located close together, they were grouped together and counted as a single colony because their foraging areas overlapped substantially. To determine which colony sites should be counted as a single colony, the half of the mean nearest-neighbor distance (ND) of observed colony sites for each year was used. If more than one colony site was located within the ND, colony censuses were carried out at each site, the data were combined and it was counted as a single colony.

Colonies have been found to have high site fidelity (Custer et al. 1980; Frederick et al. 1996); every year some colonies returned to the same locations as the previous year, some colonies were abandoned and new ones were established. To obtain the number of consecutive years (NCY) over which each colony existed at the location, the number of years between establishment and abandonment was counted. The movement of a colony was also considered and when abandonment and new establishment of colony sites occurred in neighbouring locations in successive years, the new site was assumed to be a descendant of the abandoned one, e.g. abandonment was sometimes caused by vegetation loss through natural causes or felling and the colony was often re-established nearby. The ND was used to determine a reasonable displacement distance of a colony and it was assumed that each colony had a domain of attraction of half the average distance between the next nearest sites. Thus, colonies consecutively established at the same site or at a different site within a radius of the ND were counted as a single colony. Details of the justification for applying half of the ND were explained in Chapter 4 Appendix 1. Koshida (2007)'s data was used to estimate the NCY of colonies established before 2002, consequently the NCY ranged from 1 to 36 years rather than being limiting to the period of this study.

The population of each species was calculated annually using the mean population size per colony rather than summing the population sizes for all colonies with census data. This approach was used because aerial and ground surveys produced only partial

data due to practical difficulties —problems in taking aerial photographs and/or delays in detecting colony sites. The simple sum of colony population sizes would have been inappropriate because it is an increasing function of the number of colonies with census data. The percentage of colonies surveyed increased from 78% in 2002-2004 to 94% in 2006-2011. (Data from 2005 was excluded because aerial and ground surveys were limited to only 5 out of 18 colonies). Thus, the overall total population of the target species reflect the mean colony sizes rather than the total number of individual birds in the study area.

To evaluate difference in colony size, species composition ratio, and NCY among colonies, the coefficient of variance (CV) for each year was calculated. For species composition ratio, the proportional similarity index (Whittaker 1952) was calculated for each colony every year as $\frac{\Sigma|p_i - \overline{p_i}|}{2}$, where p_i is the proportion of species i in one colony and $\overline{p_i}$ is the mean proportion of that species in all colonies surveyed in that year. The index ranges between zero and unity: zero means completely different and unity means completely equal. Then the CV of proportional similarity of the species composition ratio was obtained for each year.

Ten years are too short for ordinal time series analyses, therefore randomization tests were done to assess temporal trends in the number of colonies, population sizes of each species, sum of the population sizes of the six species, colony sizes and CVs of three variables (colony size, species composition ratio and NCY). In a randomization test, the linear regression coefficient (β) of a target variable based on the original data was obtained first. Next the year record of the data was shuffled 30,000 times and compared beta with the linear regression coefficients (β's) of the shuffled data to obtain one-sided P-values to assess whether the target variable was increasing or decreasing. Sensitivity analyses of the population of each species against the three CVs (colony size, species composition ratio, and NCY) were performed. Generalized linear models specifying population sizes of the species as explanatory variables and CVs as dependent variables were constructed, using Gaussian distribution with an identity link function for all

model fitting. The most suitable models based on Akaike's information criterion values were chosen and the coefficients of explanatory variables of the models as sensitivity against dependent variables were considered.

If the CVs of colony size and species composition ratio show parallel changes, there is a possibility that the variation in species composition ratios increased as a by-product of the increase of variation in colony sizes. To examine this possibility, a randomization test was performed to determine whether the variation in species composition ratios was solely caused by a sampling bias according to the variation in colony size. First a hypothetical total number of herons that consisted of the six species was prepared. The species composition ratio of the whole number of herons was arbitrary. Next multiple colonies with equal colony sizes from the total number of herons were sampled. Then proportional similarities of species composition ratios of these hypothetical colonies against the species composition ratio of the whole number of herons were calculated. Proportional similarities for hypothetical colonies of the same number but with different colony sizes were also calculated. Finally, the variance of the proportional similarities between equal and unequal size colonies were compared, and the probability that proportional similarities of unequal size colonies were larger than or equal to those of equal size colonies with 10,000 iterations was obtained.

To evaluate changes in nesting vegetation, the Friedman test was used to analyze whether the vegetation of colony sites changed from year to year. Nesting vegetation consisted of one or a mixture of the following three types: bamboo thickets, conifer trees and broadleaf trees; i.e., there were seven types in total.

Finally, a randomization test was performed to determine whether there was a positive correlation between NCY and colony sizes among colonies by reshuffling the year record so as to randomize the consecutive colony-size dynamics of each colony.

All statistical analyses were conducted using R ver. 2.13.0 (R Development Core Team 2013). The randomization test on the relationship between the variation in population sizes and that of species proportion ratios was also conducted with R. All R

scripts for the above statistical analyses are available from the author.

1.3 Results

During the 10-year period, there was an average of 19 colony sites in the study area every year (19.10 $\pm$ 0.72 SE colony sites, $n = 10$); cumulatively, 191 colony sites were used over the 10 years. Some colonies were in the same locations for more than one year, and a total of 62 colony sites were used (1 to 62 in Fig. 2). Colony sites were separated by an average of 13 km (mean ND over 10 years = 12.95 $\pm$ 8.39 SE km, $n = 191$), so the ND was defined as within 6.47 km. Hence, these 62 colony sites were categorized into 27 colonies (**A** to **a** in Fig. 2) because colony sites consecutively established at different locations within a 6.47 km radius were considered a single colony. Six of 27 colonies were made up of two or three colony sites in at least one breeding season, and the median distance between them was 1.44 km (range: 0.32-5.12 km, 10 combinations of colony sites in all). Finally, the annual number of colonies increased gradually (randomization test, $\beta = 0.382, P = 0.006$) from 15 to 20 (Fig. 6a)

In the case of Intermediate Egret and Black-crowned Night Heron, the average population per colony was relatively large (about 300 individuals) and these species remained dominant throughout the 10-year period (Fig. 6b). Conversely, it was small (about 50 individuals) for Great Egret and Grey Heron, and intermediate (about 100 individuals) for Cattle Egret and Little Egret. The sum of the individuals of the six species (mean colony size) ranged from 726 to 966 and did not change significantly (line with crosses in Fig. 6b, randomization test, $\beta = -4.301, P = 0.342$).

The population trends of each species varied (Fig. 6b). Grey Heron and Intermediate Egret increased (Grey Heron: randomization test, $\beta = 9.575, P < 0.001$; Intermediate Egret: $\beta = 9.519, P = 0.033$), whilst Little Egret and Cattle Egret decreased steadily (Little Egret: $\beta = -12.069, P = 0.002$; Cattle Egret: $\beta = -20.672, P < 0.001$). The Black-crowned Night Heron fluctuated over the years but remained almost constant

($\beta = 9.311, P = 0.145$). The Great Egret population was small but almost constant ($\beta = 0.036, P = 0.492$). Note that the same results were obtained when population sizes of the sum and each species in the study area were estimated by the abundance of individuals (population size per colony multiplied by the number of colonies).

Colonies were very variable in size, and the CV of colony size continuously increased (Fig. 6c) over the ten years ($\beta = 7.510, P < 0.001$). Colonies ranged from 200 to 2,000 individuals until 2004, while smaller (under 200 with minimum 8 individuals) and larger (over 2,000 with maximum 3,280 individuals) colonies appeared after 2006. Between 2008 to 2011, the smaller (under 200 individuals) and larger (over 2,000 individuals) colonies increased 33% to 41% of colonies surveyed.

In parallel with the increase in the CV of colony size, the CV of proportional similarity of species composition ratios increased (Fig. 6c), especially after 2006 ($\beta = 7.002, P < 0.001$). Until 2004, most colonies consisted of five species (Great Egret, Intermediate Egret, Little Egret, Cattle Egret and Black-crowned Night Heron), and the composition ratio was similar among surveyed colonies (mean proportional similarity = 0.86 ± 0.02 SE, $n = 43$). Grey Heron bred in only three, six and seven colonies in 2002, 2003 and 2004, respectively. Until 2004, the composition ratios of the Intermediate Egret and the Cattle Egret were higher than those of other species in half of the surveyed colonies in accordance with their large population (Fig. 6b), but no species became dominant (over 50% of the composition ratio). After 2006, 37% of all surveyed colonies were dominated by the Grey Heron, Intermediate Egret or Black-crowned Night Heron, and differences in the species composition ratios among colonies increased.

The CV of the NCY also increased gradually (Fig. 6c) ($\beta = 2.453, P < 0.001$). Eight colonies persisted between 2002 and 2011, the remainder were abandoned or newly established. Every year 1-4 colonies were abandoned and 0-3 were established. Considering the period prior to this study, 14 out of 27 colonies had existed before 2002 and 4 had persisted for over 25 years.

Table 2 shows the results of the sensitivity analyses of population of each target

species against three CVs. Population size of two to three species were detected for each CV and these explained over 90% of variation. Sensitivities of the change in population size of Grey Herons against three CVs were most intense among the six species. Increase in the CV of colony sizes was most explained by the increasing Grey Heron population. The increase in the CV of species composition ratios was also most explained by the increasing Grey Heron population, and marginally explained by the increasing Intermediate Egret population. The increase in the CV of NCY was most explained by the increasing Grey Heron population and non-changed population trend of the Black-crowned Night Heron.

The randomization test to determine whether the variation in species composition ratios increased as a by-product of the increase in variation of colony sizes did not reveal a significant result: the probability that the proportional similarities between unequally size colonies would be larger than or equal to those of equally size colonies was almost even (0.538). The increase of variation in species composition ratios could not solely be caused by the increase of variation in colony sizes.

Changes in vegetation of the colonies were significant over the years (Friedman test, $\chi^2 = 25.2, df = 6, P < 0.001$) (Fig. 7). While the vegetation in most colonies included bamboo until 2004, after 2008 more than half the colonies were located in trees.

The slope obtained by a linear regression analysis of colony sizes against NCY (43.05 $\pm$ 5.43 SE) was significantly larger ($P < 0.001$) than slopes obtained by the randomization test where the year record was shuffled for each colony so as to randomize consecutive colony-size dynamics (Fig. 8). This randomization test indicates that there was a positive correlation between colony sizes and the NCY for the colonies.

1.4 Discussion

The survey in Ibaraki prefecture from 2002 to 2011 indicated that the number of breeding colonies (average 19) increased slightly and mean colony size was almost

constant (Figs. 6a and b). These results accord well with the report by the Environmental Agency of Japan (1994): there were 20 colonies in 1992 in Ibaraki prefecture, ranging in size from 15 to 2,990 individuals (CV = 112.5), and the population of these species has been relatively constant in the area for at least two decades to 2011. However, variations in size, species composition ratio and NCY among colonies increased significantly. The majority of colony vegetation changed from bamboo thickets to trees. Colony vegetation changed from predominantly bamboo thickets to tall trees. Trends in population dynamics differed among species: Grey Heron and Intermediate Egret increased, Little Egret and Cattle Egret decreased; and Great Egrets and Black-crowned Night Herons were relatively constant —the population of both the latter species were similar to previous reports (Research Division of the Wild Bird Society of Japan 1981; Environmental Agency of Japan 1994) and unchanged for three decades. Overall, there was no significant change in population of these colonial species in the study area during the decade, but variation in the structure of colonies and population dynamics clearly increased.

In contrast to Great Egret and Black-capped Night Heron, the population of the other four species changed during the period (Fig. 6b). Grey Heron showed the greatest population growth, which is in line with earlier reports that its population is growing in other parts of Japan (Narusue 1992; Environmental Agency of Japan 1994; Matsunaga et al. 2000; Sasaki 2001). In Hokkaido, Matsunaga et al. (2000) suggested that recent climatic warming and increase in aquaculture have provided the species with additional food resources. It is not known whether the increase of this species in other more temperate parts of Japan also depends on these factors, but its ability to respond quickly to changes in food availability (Adams and Mitchell 1995) would be expected boost populations. The other increasing species, Intermediate Egret, was a predominant species in this area even though it has been designated as a 'near threatened' species in Japan (Ministry of the Environment 2002). It is not clear whether the population has been recovering due to the lack of current data from other parts of Japan, but the

abundant population in this area may be of conservation significance in Japan; monitoring of this species should continue.

Little Egret and Cattle Egret both showed a steady decline over the period (Fig. 6b); the Environmental Agency of Japan (1994) considered them to be predominant and numerous throughout Japan, including Ibaraki prefecture in 1992, and the population of both has decreased during the last two decades. Although mild winter weather contributed to their increase in France (Hafner and Fasola 1997) and rainfall drove the changes in Cattle Egret population in Australia (McKilligan 2001) and Hong Kong (Wong and Young 2006), climatic variables are unrelated to the decrease of these species in the study area because both temperature and rainfall have been almost constant (Fig. 3). It seems likely that changes in food resources or foraging habitats may be contributory factors. In northern Japan, Shimada et al. (2005) suggested that Little Egrets might be strongly affected by the increase in population of the introduced Black Bass *Micropterus psalmodies*, which had caused the decrease in the smaller native fish species they prefer. In the absence of historical and quantitative data in Japan, monitoring studies in other regions are needed to make a complete assessment of population dynamics trends of these declining species.

During 2002 and 2011, variations in size, species composition ratio and NCY increased (Fig. 6c). Since these temporal trends showed parallel changes, there is a possibility that the variation in species composition ratios increased as a by-product of the increase of variation in colony sizes; but a randomization test contradicted this possibility, and it was concluded that the observed increased variation in proportional similarities of species composition ratio could not be solely caused by the increased variation in colony size. Another change that coincided with the study period was the change in nesting vegetation; the majority of colonies changed from bamboo thickets to trees (Fig. 7). More colonies were newly established in tall trees even though bamboo thickets persisted in the area. The decrease in the number of colonies in bamboo may be due to the increase in Grey Herons because they prefer to nest near the top of tall trees.

However, such interpretation contradict the general knowledge that Grey Herons use a wide range of nest sites, including trees, bushes, reeds and on the ground. No other species shows a prominent preference for specific substrates (Kushlan and Hancock 2005). Hence, there is no strong support for the possibility that the vegetation of established colony sites affected the size or species composition ratios of colonies.

Increasing variation in NCY may help explain the increased variation in colony size and species composition ratios. The results showed that the variation in the NCY among colonies grew from year to year (Fig. 6c), and there was a significant positive correlation between colony size and the NCY that a colony existed (Fig. 8). Although food availability, measured as the area of potential foraging habitat around the colony, has often been thought to be the most important factor affecting colony size (Fasola and Barbieri 1978; Gibbs et al. 1987; Gibbs 1991; Baxter and Fairweather 1998), previous studies in this locality showed that variables related to foraging sites (areas around ponds, rivers, paddy fields and lotus fields) did not have a major impact on colony size; instead the NCY had a significant positive relationship with colony sizes (Fujioka et al. 2001; Tohyama 2005). Increasing variation in a colony's size is therefore closely related to the colony's longevity. As for increasing variation in species composition ratio among colonies, variations were due to the occurrence of colonies dominated by Grey Heron, Intermediate Egret, or Black-crowned Night Heron after 2006. In particular, the dominance of Grey Heron was prominent in small, recently established colonies (Fig. 8). It is well known that the Grey Heron often breeds in small colonies of only 2-10 nests, while the other five species are gregarious and usually breed in large mixed-species colonies (Kushlan and Hancock 2005). Thus, the Grey Heron population growth after 2007 might contribute significantly to the increasing variation in the species composition ratio and colony size (Table 2) despite its relatively small overall population.

Overall, the local population of herons and egrets in eastern Japan seems to have remained constant for at least the last decade, in parallel with the constant climate and land use variables. None-the-less, population dynamics of constituent species have been

changing, and variations in colony sizes and species composition ratios have also increased. Long-term and comprehensive colony censuses have enabled us to reveal such changes. Consecutive studies are required not only to reveal the factors affecting the population dynamics of each species at a regional level, but also for a better understanding of relationships between each species' population and the sizes or composition ratios of mixed-species colonies.

Chapter 2

Close-proximity Stress against Newcomers: Spacing Mechanisms of Heron Colonies

Note: Since this chapter is in preparation for submission to a scientific journal, I include summary instead of full manuscript.

2.1 Summary

Colonial birds usually form their breeding colony apart from neighboring colonies so as to avoid overlap of foraging sites among them. Even distribution is well documented in the region where available nesting and foraging area are distributed in one-dimensional regions like coastlines. However, in two-dimensional regions like lowland plains, colony distributions are hardly distinguished from random null distributions even with spatial analyses incorporating random point processes such as Ripley's K and L functions. Here I proposed a new method for analyzing spacing pattern of colony sites using 28-year data of heron colony distribution around Ibaraki Prefecture from 1986 to 2013. For each year, I evaluated the repulsive force against each colony site from all surrounding colony sites by summing up their inter-colony distance considering inverse-square law of physics. Ninety-five percent of annual colony sites during the 28 years experienced a similar strength of repulsive force, while the remainder experienced extremely strong repulsive forces. New colony sites that were formed at new locations where there had

been no colony site in the previous year suffered stronger repulsive forces than did reused colony sites that were formed at the same locations as in the previous year. The repulsive force of a colony site did not decrease during its persistence period, and colony sites that were established at locations with weak repulsive forces persisted longer than those that were established at locations with strong repulsive forces. These results were not affected even when the repulsive force was weighted with colony size or persistence period. Spacing of heron colony sites is controlled only by the distance between them. I discussed how heron and egret individuals recognize spatial repulsion among colony sites and consider its reciprocal, attractive force.

Chapter 3

Collective Philopatry in Mixed-species Heron Colonies

Note: Since this chapter is under review in a scientific journal, I include summary instead of full manuscript.

3.1 Summary

Many animals are faithful to their natal sites and return to breed at the same locations every year. Colonial seabirds exhibit a high degree of site fidelity, and breeding colonies on the same cliffs or islands are reused for many years. However, seabirds are obliged to reuse colony locations because available breeding sites are often restricted. In contrast, herons and egrets form colonies on comparatively unrestricted breeding sites such as trees or bamboo thickets, and individuals return to their natal colonies less frequently. I examined whether heron colonies exhibit site fidelity despite herons being facultative reusers of previously occupied colony locations. Sixty-one colonies that were formed throughout Ibaraki Prefecture in Japan from 1963 to 2013 were classified based on their persistence period and whether they had shifted locations. Ten colonies existed for only one year, not exhibiting site fidelity. Twenty-five colonies reused the same locations and had persisted for more, thus exhibiting site fidelity. The remaining 26 colonies persisted but shifted to nearby locations when their former sites were destroyed. Their site fidelity was evaluated based on the distance between a focal point and the last location of their movement pathway. This distance for 16 colonies was shorter than null expectations,

revealing site fidelity in a broader sense because they had remained within a small area rather than moving far away. Consequently, 41 out of 61 colonies (67%) exhibited site fidelity. Despite an abundance of available breeding sites, heron colonies were likely to return to the exact location of or near previous sites. I call this facultative site fidelity at the colony level as collective philopatry. A high rate of collective philopatry may originate from a few faithful pioneer individuals with many others following them.

Chapter 4

An Expanding Species Promotes the Persistence of Mixed-species Heron Colonies

4.1 Introduction

The introduction and spread of exotic species has become a global ecological and conservation crisis as invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Elton 1958; Vitousek et al. 1996; Wilcove et al. 1998; Gurevitch and Padilla 2004). Negative effects of invasive species on native communities have been extensively reported when the invasion was driven by human transport and commerce (Ruiz et al. 1997; Mack et al. 2000). Similar problems occur with range expansion of indigenous species. Expanding species can cause an interspecific competition with native species especially where those species breed in spatially limited areas. In bird breeding colonies where hundreds of individuals nest close to one another, competition for food or nesting-habitat resources should become intense.

In mixed-species colonies of seabirds, increasing and expanding species have been associated with decreases in the breeding populations of other species because interspecific competition for restricted nest-sites, such as cliffs and islands, is severe (Trivelpiece and Volkman 1979; Quintana and Yorio 1998). For instance, the rapid increase and expansion of Herring Gulls (*Lurus argentatus*) displaced another co-existing gull species from their colony sites because Herring Gulls have the competitive

advantages of larger body size and earlier arrival to the colony site (Burger and Shisler 1978). Past studies have shown that in terrestrial areas, the expansion of Cattle Egrets (*Bubulcus ibis*) causes direct competition with other heron and egret species for nest sites and nesting materials. Even though the presence of abundant suitable habitat areas adjacent to colonies suggests that colony sites are not a limiting factor (McCrimmon 1978), aggressiveness and the highly gregarious nature of Cattle Egrets excluded other species from high-quality nest sites (Burger 1978; Dami et al. 2006).

Gregarious colonial birds, like Cattle Egrets, often rely on the nesting activities of other species as a stimulus for their own nesting and breeding, and individuals seldom establish new colonies independently (Rice 1956; Dusi and Dusi 1968; Westerskov 1974; Belzer and Lombardi 1989). There are pioneer/follower or producer/scrounger relationships (Ohtsuka and Toquenaga 2009a; Ohtsuka and Toquenaga 2009b) in the formation of mixed-species colonies. Species that arrive later in the season refer to the presence of those that arrived earlier as a cue for profitable breeding sites (Dusi and Dusi 1968; Westerskov 1974). Unlike territorial breeding birds that can select their nesting sites individually, colonial birds prefer consensus when establishing their colony sites. Forming a new colony requires a time-consuming process of group decision making, and individual colonial birds may be reluctant to pioneer new colonies where conspecifics are absent (Parker et al. 2007). Thus the continuous reuse of a colony site, rather than frequent changes in site location, is beneficial for individual birds because they can save their time of group decision making.

If an expanding species is skilled at establishing new colonies and has been expanding by forming its own new colonies rather than by joining the existing colonies of other species, the incorporation of a new species into mixed-species heron communities might lead to positive consequences in regards to the formation and persistence of colonies. The distribution range and population size of the Grey Heron (*Ardea cinerea*, Ardeidae) markedly increased in Japan over a span of 20 years (Environmental Agency of Japan 1994; Matsunaga et al. 2000; Sasaki 2001). Grey Herons are native wading birds that

exist throughout temperate Europe, Africa and Asia (Kushlan and Hancock 2005). They have begun to breed in Japan by establishing new colonies or by joining existing colonies established by other species (Environmental Agency of Japan 1994; Sasaki 2001). In this study, I examined the effect of the recent population increase and expansion of Grey Herons on the formation of mixed-species heron colonies in Japan. Since suitable nesting habitats are not restricted and no direct negative interspecific interactions like predation or aggressive behavior have been documented between Grey Herons and the species they share breeding sites with (Environmental Agency of Japan 1994), I expected that Grey Herons may facilitate the establishment and persistence of heron colonies based on the following two ecological features.

First, Grey Herons have the most solitary habits among the six colonial heron species in Japan. The Grey Heron is primarily a colonial nesting species, but it often breeds in small, single-species colonies of 2-10 nests (Environmental Agency of Japan 1994; Kushlan and Hancock 2005). Grey Herons have the potential to establish new colonies without relying on existing colonies established by other species. In contrast, the other five species usually breed colonially, mostly in large mixed-species colonies of 50-3,000 individuals (Environmental Agency of Japan 1994). Second, Grey Herons arrive at colony sites and begin nesting about a month before the other species. This head start may serve as a cue for the other, later-arriving species in choosing their colony site (Sepptänen et al. 2007). If a colony site has degraded and become unsuitable for breeding, Grey Herons may choose an alternative location near the former site earlier than arrival of the other species, and hence, the mixed-species colony can persist.

In order to clarify whether the recent population increase and expansion of Grey Herons have affected interspecific dependency in regards to colony site choice, I analyzed 16-years monitoring data on mixed-species colonies around Ibaraki Prefecture, Japan, which include periods before and after the expansion of Grey Herons. I predicted that if Grey Herons had begun to take an initiative in establishing colonies and other species had begun to follow them in colony-site selection, more colonies including Grey Heron

individuals would have been newly established and persisted longer than colonies without Grey Heron populations. I focused on three colony states, establishment, persistence and abandonment, and evaluated (1) the changes in the number of establishment and abandonment events of colonies before and after the expansion of Grey Herons, and (2) the differences in the persistence periods of colonies between those with and without Grey Heron populations. Results show that (1) after the Grey Heron expansion, more than half of colony establishments were pioneered by Grey Herons, and the number of abandonments decreased, and, (2) colonies with Grey Herons had a greater propensity to persist, whereas those that had never included Grey Herons were prone to being abandoned. This study illustrates the positive effects of the presence of a newcomer species on mixed-species colony dynamics.

4.2 Methods

Study area and species

In Japan, six species of colonial herons and egrets are distributed: Great Egret (*A. alba*), Intermediate Egret (*Egretta intermedia*), Little Egret (*E. garzetta*), Eastern Cattle Egret (*B. coromandus*), Black-crowned Night Heron (*Nycticorax nycticorax*), and Grey Heron (*A. cinerea*). Nationwide research in 1980 (Research Division of the Wild Bird Society of Japan 1981) and 1992 (Environmental Agency of Japan 1994) reported that colonies were distributed throughout lowlands in Japan and their species compositions, except in Hokkaido, were mainly all or some of the five species, with the exclusion of Grey Herons. Distribution of Grey Herons around the 1950-1970s was partial, and their colonies were mainly located in Hokkaido and along the Sea of Japan (Kurata and Higuchi 1972; Sawara et al. 1994). The total proportion of the Grey Heron among all the colonial herons and egrets in Japan was 5.5% in 1980 (Research Division of the Wild Bird Society of Japan 1981). Since then, Grey Herons have markedly increased in range and population size, and have recently been distributed in both coastal and inland areas

throughout Japan (Environmental Agency of Japan 1994; Matsunaga et al. 2000; Sasaki 2001). Currently there is no conclusive explanation for the Grey Heron expansion. The introduction of Largemouth Bass (*Micropterus psalmodies*) and Smallmouth Bass (*M. dolomieu*) in lakes and rivers from 1972 for leisure fishing (Kaneko and Wakabayashi 1998) might provide Grey Herons with their preferred feeding choices, large fish, even inland, but there are no quantitative data to support this hypothesis.

The study area and species were the same as described in Chapter 1. Population census data with aerial photographs and ground surveys for the number of each species in the study area were available for 2002 to 2011 (Mashiko and Toquenaga 2013) and census data for 2012 were collected by the author. Trends in the population sizes of each species varied (Fig. 9). The populations of Great Egrets and Black-crowned Night Herons remained relatively constant, while those of Grey Herons and Intermediate Egrets increased and those of Little Egrets and Cattle Egrets decreased. A full description of the methods for population census and data analyses is described in Chapter 1. For the variation in breeding season among the six species, see Fig. 4 in Chapter 1.

Colony data

Colony sites in the study area have been recorded over the last 30 years. Koshida (2007) reported that those colonies showed high site fidelity: an average of 75% of colony sites were formed at the same sites as in the previous year. When a colony was abandoned, checks were made to determine whether other colonies had formed nearby. In order to minimize missing information for colonies, I used local literature and personal information from local observers especially during periods in which surveys by the members of the Population Ecology Laboratory were not intensive.

Until 1999, all colonies were composed of five species and excluded Grey Herons, with the exception of one colony in which Grey Herons had been nesting with the other five species (colony 3 in Fig. 10). The first colony established by Grey Herons alone was recorded in 2005 (colony 35 in Fig. 10, Mashiko and Toquenaga 2013). Thus, I defined

2005 as the beginning of the increase and expansion of Grey Herons in the study area. Since my data extended to 2012, and for a balanced pre/post examination, I compared data for eight years before (1997 to 2004) and after (2005 to 2012) the Grey Heron expansion. The mean population size of Grey Herons per colony in the study area in 2012 was 188 individuals, which was 9.6 times larger than that of 2004 (line with filled triangles in Fig. 9).

Location shifts of colony sites were considered in the same manner as described in Chapter 1 and 3. Details of the justification for applying half of the ND were explained in Appendix 1. From 1997 to 2012, two neighboring colony sites were separated by an average of 12.78 $\pm$ 1.85 km every year. Thus, when abandonment and new establishment of colony sites occurred within a radius of 6.39 km in the same year, I assumed that the new colony site was a descendant of the abandoned one and denoted it as the same colony. A colony was deemed to have been established when a new colony site was located where there had been no colony site within a radius of 6.39 km in the previous year. A colony was deemed to have been abandoned when no new colony site was located within a radius of 6.39 km in the next year. A colony can be characterized by three states: establishment, persistence and abandonment. The persistence period is the duration between establishment and abandonment.

Each colony record consists of the establishment and abandonment years, accompanied by species compositions or counts for each year. Aerial photographs and ground surveys for species proportions were conducted from 2002 (Mashiko and Toquenaga 2013), and hence yearly colony size and species composition of constituent species are available for each colony since 2002. For data before 2001, no census data with aerial photographs was taken, but binary values (0: absent, 1: existing) for constituent species are available. The species compositions of almost all colonies that existed earlier than 2002 were reported in earlier studies (Fujioka et al. 2001; Koshida 2007); these data were obtained by observing the nesting activities or going inbound and outbound movements of each species in the colonies from the ground. In this study, I

evaluated the incorporation of Grey Herons into heron colonies using binary values for the existence of Grey Herons: with or without Grey Herons in the species compositions of the colonies. The five constituent species other than the Grey Heron were combined because they were included in 88% of all recorded mixed-species colonies.

Statistical analyses

To examine whether the incorporation of Grey Herons into existing colonies played a role in facilitating the persistence of colonies, it might be straightforward to perform Generalized Linear Model (GLM) analyses with the persistence period of each colony as the dependent variable. However, while each colony has a persistence period, they have different numbers of explanatory variables of Grey Heron existence or species proportions according to the persistence period. Preliminary survival analyses using the mean proportions of each species or Grey Heron existence as explanatory variables failed to show consistent and conclusive results (Appendix 2). This failure was caused by the lack of consideration of a phase transition: the number of colonies with Grey Herons was not constant but clearly increased after 2004 (Fig. 10). After observing the phase transition, I performed more blunt statistical analyses, simple chi-squared analyses to examine the effect of Grey Heron expansion on colony establishment and abandonment. When this blunt approach showed significant results, more sophisticated and complicated analyses were not required.

In order to detect whether the number of establishment and abandonment events of colonies had changed before and after the expansion of Grey Herons, I performed a 2×2 chi-squared test. To analyze the colony establishments, I counted the number of establishment events and categorized them into two classes: with or without Grey Heron populations in the first year of the colony. To analyze the colony abandonments, I counted the number of abandonment events according to the year when the abandonment was recorded. For abandonment events in 1997, I referred to the data for the four colonies that existed in 1996 (colonies 15, 19, 20, and 21 in Fig. 10). Then I focused on the binary-state species composition during the persistence periods of those

abandoned colonies and classified them into four categories: Grey Herons existed throughout the persistence period (Grey Heron throughout: T), Grey Herons joined after the establishment of colonies (Grey Heron post-establishment: P), Grey Herons never joined (Grey Heron nonexistent: N), and Grey Herons had joined the colony but disappeared before abandonment (Grey Heron disappeared: D).

In order to examine whether the incorporation of Grey Herons affected the length of persistence periods of colonies, I classified all colonies into the same four categories as those in the analysis of abandonment (T, P, N and D) and compared their survival curves. Since the datasets for persistence periods contained censored data ("+" in the persistence period in Fig. 10), non-parametric survival curves were estimated with the Kaplan-Meier method for each category. Differences between the curves were evaluated with the log-rank test. The persistence periods for all colonies were obtained from Koshida (2007), Mashiko and Toquenaga (2013), and a 2012 census conducted by the author. Seventeen out of 39 colonies started before 1997 but were not abandoned in 1997. To each colony I assigned its actual persistence period rather than limiting it to my study interval (1997 to 2012).

Since there was only one colony for which the binary-state species composition data was not available (colony 36 in Fig. 10), 39 colonies during 1997 to 2012 were used to analyze the establishment and persistence periods, and 43 colonies, including four colonies in 1996, were used to analyze the abandonment. All statistical analyses were conducted with R version 3.0.1 (R Development Core Team 2013).

Expectations for the analyses of establishment and abandonment

Before the Grey Heron expansion, while some colonies were newly established without Grey Heron populations (open circle in Fig. 11a), almost no colonies with Grey Heron populations were newly established (filled circle in Fig. 11a) because the distribution of Grey Herons itself in the study area was still limited. Possible changes in the number of establishments without Grey Herons before and after expansion could fall under any of three patterns: increasing, unchanged, or decreasing (dashed arrows in Fig. 11a), while

colonies with Grey Herons would fall under either of two patterns: increasing or unchanged (solid arrows in Fig. 11a). I excluded the increasing pattern in colonies without Grey Herons (X-marked dashed arrow in Fig. 11a) as it was unlikely to occur given that the total number of colonies in each year did not change before and after Grey Heron expansion (17.5 ± 0.7 SE in before and 18.8 ± 0.3 SE in after, Fig. 10). Therefore, a total of four combinations of changing patterns were possible (Figs. 11b, 11c, 11d and 11e).

I predicted that if the number of newly established colonies without Grey Herons showed an unchanged pattern (open circles with a dashed lines in Figs. 11b and 11c), the other species were showing an aversion to the early arrival of Grey Herons in their colonies possibly because breeding in a mixed-species colony with Grey Herons may result in negative consequences such as low reproductive success, and thus, the number of newly established colonies would remain the same even after the expansion of Grey Herons. Conversely, I predicted that if the number of newly established colonies without Grey Herons showed a decreasing pattern (open circles with dashed lines in Figs. 11d and 11e), the other species were showing a preference for following the early arrival of Grey Herons possibly because it may save them time and effort in colony site selection, and thus, they may cease to establish new colonies on their own. On the other hand, the number of newly established colonies with Grey Herons should remain unchanged when Grey Heron expansion involves colonies that have already been established by other species (filled circles with solid lines in Figs. 11b and 11d), but should increase when Grey Heron expansion involves their own establishment of new colonies (filled circles with solid lines in Figs. 11c and 11e).

Regarding abandonment, I predicted a decreased pattern of abandonment if colonies without Grey Herons (N and D) were abandoned at the same frequency as before (open circles with dashed lines in Figs. 11d and 11e) given that colonies without Grey Herons had an absolute majority in the total number of observed colonies before, but not after, Grey Heron expansion. However, if the pattern were unchanged (open circles with

dashed lines in Figs. 11b and 11c), the frequency of abandonment of colonies without Grey Herons (N and D) must have increased after Grey Heron expansion. On the other hand, the number of abandoned colonies with Grey Herons (T and P) should remain unchanged when those colonies did not abandon (filled circles with solid lines in Figs. 11b and 11d). However, it should increase when colonies with Grey Herons had abandoned in the same way as colonies without Grey Herons (filled circles with solid lines in Figs. 11c and 11e).

4.3 Results

From 1997 to 2012, between 15 and 22 (18.1 $\pm$ 0.4 SE) annual colonies were observed every year, and a total of 40 colonies were recorded. The persistence periods ranged from 1 to 50 years (Fig. 10).

Changes in the number of colony establishment events showed an increasing pattern in colonies with Grey Herons, but a decreasing pattern in colonies without Grey Herons (Fig. 12a), which corresponded to the expectation represented by Fig. 11e. The total number of colony establishment events declined only by two after the Grey Heron expansion (Fig. 12a), whereas the number of colonies established with Grey Herons significantly increased after the expansion (chi-squared test, $\chi^2 = 6.712, P = 0.019$); 60% of colony establishments were replaced by colonies with Grey Herons (Fig. 12a'). Before 2004, only one colony (colony 33 in Fig. 10) included Grey Herons in its the establishment year, but this colony consisted of six species. It was not clear whether the Grey Heron led the establishment of this colony because of the lack of information from its onset. Conversely, after 2005, the establishment of six colonies (colonies 35, 39, 41-44 in Fig. 10) was obviously led by Grey Herons. Five of these (all except colony 41) were established by Grey Herons. Colony 41 was relatively small and dominated by Grey Herons (12 nests); they gathered at the colony site from the very beginning of the breeding season, and a smaller number of Black-crowned Night Herons (4 nests) were

observed during the late breeding season. Grey Herons established their colonies irrespective of existence of the other species, but the other heron species almost ceased establishing their own colonies.

The number of abandonment events had an unchanged pattern in the colonies with Grey Herons and a decreasing pattern in colonies without Grey Herons (Fig. 12b), which corresponded to the expectation represented by Fig. 11d. These results reflect that the colonies without Grey Herons (N and D) were abandoned at the same frequency as before, whereas the colonies with Grey Herons were seldom abandoned. Abandonment mainly occurred in colonies without Grey Herons (N) both before and after the Grey Heron expansion (Fig. 12b', chi-squared test, $\chi^2 = 2.214, P = 0.319$). Since 2005, there have been abandonment events in both T and D categories. The total number of abandonment events decreased dramatically, nearly halved, after the Grey Heron expansion.

Among the four categories (T, P, N and D), I excluded D in the following analysis of the persistence period because category D included only a single colony, and hence, was not suitable for the survival analysis. Survival curves differed between the T and N categories: persistence periods of colonies with Grey Herons were much longer than those without Grey Herons (log-rank test, $\chi^2 = 4.7, P = 0.030$; Figs. 13a and 13c). Survival curves also differed between the P and N categories: persistence periods of colonies joined by Grey Herons were much longer than those without Grey Herons (log-rank test, $\chi^2 = 14.2, P < 0.001$; Figs. 13b and 13c). Survival curves did not drop for decades for colonies with Grey Herons. Conversely, survival curves for colonies without Grey Herons continuously decreased, and those colonies lasted 25 years at most.

4.4 Discussion

Recent population increases and expansion of Grey Herons have changed the dynamics of establishment, persistence and abandonment of mixed-species colonies in the study

area. By comparing colonies with and without Grey Herons, I found that (1) after the Grey Heron expansion, more than half of the colony establishments were led by Grey Herons, and the number of abandonments decreased. (2) Colonies with Grey Herons had a greater propensity to persist, whereas those that had never included Grey Herons were prone to be abandoned.

Two ecological features of Grey Herons, the highest rate of solitariness and the earliest arrival order among the six species of herons and egrets, are likely to contribute to the establishment of colonies. Although there were few differences in the total number of newly established colonies between pre- and post-expansion, Grey Herons have begun to take over the task of colony establishment since its expansion, as more than half of the establishments were led by Grey Herons after 2005 (Fig. 12a). Its solitary habits would enable this species to newly establish small, single-species colonies. In fact, all six colonies containing Grey Herons established after 2005 were relatively small and made up of only Grey Herons or dominated by them (Mashiko and Toquenaga 2013). Moreover, their arrival time at the beginning of the breeding season, which is the earliest of the six species, enables them to choose colony sites independently. Thus, Grey Herons began to take over the role of vanguard for establishing colonies at locations where no herons or egrets have bred in the past.

The participation of Grey Herons allowed the other five species to adopt a new strategy for colony site selection: joining colonies established by Grey Herons at the very beginning of a breeding season. This new strategy has been adopted by the five species since 2005 when the population of Grey Herons began to increase. Therefore, the number of newly established colonies formed only by the five species arriving later in the breeding season decreased after 2005 (Fig. 12a). This strategy becomes optimal when identifying resources or establishing a colony costs more than scrounging or following a pioneer species (Ohtsuka and Toquenaga 2009a; Ohtsuka and Toquenaga 2009b).

In Japan, the Great Egret, Intermediate Egret, Little Egret, and Eastern Cattle Egret have never formed single-species colonies consisting of less than 50 individuals

(Environmental Agency of Japan 1994). Among them, the Eastern Cattle Egret, an especially gregarious species (Kushlan and Hancock 2005), often relies on the nesting activities of other species as a stimulus for their own nesting and breeding (Rice 1956; Dusi and Dusi 1968; Westerskov 1974; Belzer and Lombardi 1989). Moreover, in colonial seabirds, individuals often fail to colonize new habitats because of their strong colony-site philopatry (Parker et al. 2007). Artificial stimuli, such as decoys, recorded vocalizations and mirrors, are often used to encourage new colonization or restoration of abandoned colony sites (Jones and Kress 2012). Similarly, in my study the incorporation of Grey Herons act as a stimulus for other gregarious species in choosing their breeding-colony sites. Although the five late-coming species could establish their own colonies without Grey Herons, following a vanguard species remains the easiest alternative.

This pioneer/follower relationship among the constituent species of mixed-species colonies also explains the present results for abandonment and persistence period (Figs. 12b and 13). Abandonment of colonies was sometimes caused by the disappearance (either through natural death or felling) of nesting vegetation. When individual herons and egrets are confronted with these situations, they can either establish a new colony near the previous one or abandon the site and join another colony that has already been established by other individuals but is located far from their previous site. Trees and bamboo thickets are abundant and exist throughout the study area. It is easy for Grey Herons to establish a new colonies, but not so for more gregarious species. When Grey Herons establish a new colony in the vicinity of past colonies of other species, the remaining species often opt to join that colony. Consequently, a past colony is not abandoned, but persists for at least another year. This is why colonies perpetuated the Grey Heron hegemony once they became a constituent species.

Several studies of territorial breeding birds have demonstrated that individuals of earlier-arriving species can be used as informants by the later-arriving species. In tit and flycatcher species in northern Europe, the presence and density of resident species

were used by migrant species as a source of information on breeding patch and nest-site quality (Mönkkönen et al. 1990; Mönkkönen et al. 1999; Thomson et al. 2003). Since many bird species rush to choose their breeding location, following earlier-arriving species is an effective strategy for later-arriving species in order to save time (Sepptänen et al. 2007). In colonial breeding species, individuals also refer to the presence of other species as a source of information for choosing their colony site (Dusi and Dusi 1968; Westerskov 1974). However, using the presence of other individuals as a cue is not always beneficial; consequences would vary depending on the types of interspecific relationships that develop from the ecological features of constituent species, such as arrival order, aggressive behavior and predation.

In my case, direct negative interspecific interaction such as predation and aggressive behavior was not observed between Grey Herons and the other five species. Thus, Grey Heron expansion has led to a positive consequence: local populations of colonial herons and egrets seems to have gained the benefit of colony sustainability. If the positive effects of Grey Heron expansion are universal, the three states of mixed-species heron colonies in Japan will be likely to change according to my results: colonies with Grey Herons are established more frequently and persist longer, whereas most colony abandonments occur when Grey Herons are absent. However, this does not necessarily indicate that the incorporation of Grey Herons has led to an increase in the population size of the five species formerly dominant in Japan. In fact, population sizes of Little Egrets and Eastern Cattle Egrets have decreased since 2002 in my study area (lines with open triangles and diamonds in Fig. 9); however, the factors contributing to this decrease in population size are not yet clear. Relatively little is known about the effects of rapidly changing numbers and distribution of one species against another (cf. Burger 1978; Werschkul 1978; Dami et al. 2006). It remains a challenge for future studies to determine whether the expansion of Grey Herons has to negative impacts on other species by reducing their reproductive success.

In the present study, I found that recent population increases and expansion of Grey

Herons in Japan have been promoting the persistence of heron and egret colonies. The positive consequences on heron colonies led by Grey Heron expansion are unique, and contradict the negative effects of expanding species on communities have been extensively reported (Mack et al. 2000). However, if Grey Herons had different characteristics, such as gregariousness or later arrival order compared to the other colonial herons and egrets, the outcome of their expansion would be more detrimental to other species. Interspecific interaction has important consequences on the community ecology and conservation (Sepptänen et al. 2007). The ecological features of an expanding species are crucial factors in determining whether they infringe upon or are suitable for co-colonization, especially when they share the same resources.

4.5 Appendices

Appendix 1: In general, each colony site has a spatial repulsive force that creates distance between itself other colonies in order to reduce the overlapping of foraging ranges surrounding each colony site. I supposed that each colony site had a domain of attraction of half the average distance between its nearest sites every year. I calculated the average of nearest-neighbor distance of colony sites every year from 1997 to 2012 and it was 12.78 $\pm$ 1.85 km. Thus, when abandonment and new establishment of colony sites occurred in the same year within the half-distance of 12.78 km, i.e., 6.39 km, I assumed that the new colony site was a descendant of the abandoned one and denoted this as persistence. A colony was deemed abandoned when no new colony was located within a radius of 6.39 km.

Figure 14 is a histogram of displacement distances when colony-site shifts were recorded ($n = 63$). It shows a converse J-shaped pattern and the median is 2.08 km. Herons and egrets fly at an altitude of 50-70 m when searching for new colony sites, and it is plausible that they can see to a distance of 2 km.

I believe that 6.39 km not a quite large distance as maximum distance for

determining colony-site shift because the foraging range of herons and egrets in breeding season in the study area is usually further than a radius of 6.39 km around the colony site: foraging ranges have radii of about 10 km, and sometimes over 20 km (Nabeya 2011). If I assume that the foraging range (r, solid line in Fig. 15) has a radius of 10 km from each colony site and the displacement distance (d, bold line) between an abandoned colony site (A) and a newly established colony site (B) is 6.39 km, 60% of the foraging range (shaded area) overlaps between them (the diagonal-hatched area is $\int_{d/2}^{r} \sqrt{r^2 - x^2} dx$, thus the proportion of shared area to B's foraging range is $\frac{4\int_{d/2}^{r} \sqrt{r^2 - x^2} dx}{\pi r^2}$). Therefore, I believe it is practical to assume that individual herons and egrets breeding in either abandoned or new colony sites may use the same foraging area.

Appendix 2: Colony data includes the censored data for colonies that persisted at least until 2012. For this reason, I performed the survival analyses. For all colonies since 1997, I used the binary variable of Grey Heron (*Ardea cinerea*) existence. I calculated the mean proportions of Grey Heron existence and coefficients of linear regressions of the binary values. The latter variable represents the change in Grey Heron existence during the persistence period of the colony. For the colonies since 2002, I used aerial photographic counts (total number of all species, except Black-crowned Night Herons (*Nycticorax nycticorax*), or colony size) and ground surveys for proportions of all six species (Chapter 1). I calculated the mean aerial photographic counts and mean proportions of each species for the data since 2002. I first performed survival analyses for the persistence periods against the mean proportions and change in Grey Heron existence for the colonies existing from 1997 to 2012. I also performed survival analyses of the persistence periods against the mean colony sizes and mean proportions of six heron and egret species for the colonies existing since 2002.

I used logistic distribution for parametric survival analysis with the "survreg" function in the "survival" library in R. I also tried the Cox proportional hazard models with the "coxph" function in the "survival" library in R. Table 3 shows the results of

survival analyses with the parametric and the Cox proportional hazard functions for colonies existing from 1997 to 2012. I calculated both the AIC values and R^2 values based on Nagelkerke (1991) for model comparisons. AIC values of the Cox proportional hazard models were always lower than those of the parametric survival analyses. The best Cox proportional hazard model indicated negative effects of the mean proportions of Grey Heron existence against colony persistence. Colonies with Grey Herons tended to persist for longer but the reverse was true for the parametric survival analyses. Changes in Grey Heron proportions did not explain the persistence of colonies.

The Cox proportional hazard models showed lower AIC values than those of the parametric ones for the colonies since 2002 (Table 4). Colony size and population sizes of Eastern Cattle Egrets (*Bubulcus coromandus*) and Black-crowned Night Herons were the significant explanatory variables. If a colony was small, but included less Eastern Cattle Egrets and more Black-crowned Night Herons, then the colony tended to persist for longer. However, the reverse was true for the parametric survival functions.

General Discussion

In this study, I investigated the colony dynamics of herons and egrets from ecological and historical perspectives based on 51 years of data for colonies around Ibaraki Prefecture, Japan. In Chapter 1, I summarized the results of the 10-year colony censuses. From 2002 to 2011, the local population of herons and egrets in the study area seems to have remained constant, but population dynamics of constituent species have been changing, and variations in colony sizes and species composition ratios have also increased. This is the third report showing the long-term regional population dynamics of heron colonies in Japan. It provides important information for future assessment of the population status of colonial herons and egrets in Asia.

In Chapter 2, I clarified the spacing mechanisms underlying the distribution of colonies. In contrast with the failure to distinguish even, random or clumped distribution using acknowledged methods of spatial point pattern analyses, evaluating the repulsive force against each colony from all surrounding colonies in each year was effective in detecting spacing patterns of colonies. Results show that most colony sites from 1986 to 2013 maintained relatively consistent distances from each other, and new colony sites experienced stronger repulsive forces than did reused colony sites. New colony sites that were established in locations distant from neighboring colony sites persisted for longer periods of time. These results suggest that colonies exhibit a preference to sites with low repulsive forces at the same or nearby locations as in previous years.

In Chapter 3, I used 51 years of data for colonies to demonstrate that a total of two thirds of colonies exhibited site fidelity by relocating to the same sites over many years or by remaining within small areas rather than moving far away. Despite an abundance of available breeding sites, heron colonies were likely to return to the exact location of or near previous sites. This study represents the first application of random walk models to the measurement of site fidelity of moving bird colonies. It provides a first step toward investigating site fidelity at the population level.

In Chapter 4, I discussed how recent population increases and expansion of *A. cinerea* have been promoting the persistence of heron and egret colonies, and how local populations of colonial herons seemed to gain the benefit of colony sustainability. After their expansion, *A. cinerea* began to take the initiative in establishing colonies, and other heron species followed them in colony site selection. The positive consequences for heron colonies led by *A. cinerea* expansion may be unique given the fact that negative effects of expanding species on communities have been extensively reported (Mack et al. 2000).

This study illustrates that the presence of pioneers has played an important role in the persistence of colonies by considering *A. cinerea* as a pioneer. But this pioneer/follower or producer/scrounger relationship would have been employed by heron and egret individuals for choosing breeding colonies since before the expansion of *A. cinerea*. The pioneer/follower relationships can be considered universal in group-living animals. In many animals that forage or travel in groups, a few individuals have pertinent information such as knowledge of the location of a food source or of a migration route, but this is sufficient to produce effective leadership and lead to collective decisions (Couzin et al. 2005).

When conservation and management plans are needed for group-living or gregarious animals, it is important to understand the characteristics of the pioneer and follower. For instance, the large wading birds *C. boyciana* (Oriental Stork) and *N. nippon* (Crested Ibis) once became extinct in Japan; but thanks to conservation efforts, they have now been reintroduced and are breeding again in a portion of their natural ranges (Naito and Ikeda 2007; Ministry of the Environment 2013). In China, where wild populations of these birds exist, they breed in single-species colonies (Dong-Ping et al. 2003; Zan et al. 2008). The populations of these birds reintroduced in Japan are still too small to form breeding colonies, but understanding who pioneers new colonies or how to foster pioneer individuals would be helpful to succeed in the reintroduction project and the establishment of reintroduced individuals in nature.

The results of this study are the product of the compilation of colony data around

Ibaraki Prefecture over a span of about 50 years. I have not yet compared the current results with other regions in Japan due to a lack of compiled data sets for colonies in other regions. Although long-term local population trends of herons and egrets have only been reported by Narusue (1992) and Matsunaga et al. (2000), I believe that there are numerous unpublished records of colonies in various areas of Japan. Establishing a baseline data set by mapping the distribution of colonies and taking censuses of breeding populations are the main priorities for conservation of herons in East and Southeast Asia (Kushlan and Hafner 2000). The compilation of local literature followed by the establishment of a network of organizations and people who are involved in heron research and conservation in the whole of Japan and in Asia is necessary to further our understanding of the colony dynamics and population status of herons and egrets in Asia.

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Table 1 Meaning of the term "colony" and representation of the duration of colony from establishment to abandonment in each chapter

Chapter	Meaning of the term "colony"	Representation of the duration of colony from establishment to abandonment
1	Lineage	Number of consecutive years (NCY)
2	Colony site	Persistence period
3	Lineage	Persistence period
4	Lineage	Persistence period

Table 2 Sensitivity of population sizes against CVs. βs are coefficients of the generalized linear models that examined the effects of the population size of each species (explanatory variables) on three CVs (dependent variables) using the data from 2002 to 2011 with Gaussian distribution and identity link function. P values were derived from Wald test. ΔAIC shows the difference in AIC from the best models

DV [a]	Model	Explanatory variables										ΔAIC	R^2 [b]
		GH [c]		GE [d]		IE [e]		LE [f]		CE [g]		BNH [h]			
		β	P	β	P	β	P	β	P	β	P	β	P		
CS [i]	1	0.351	0.054					−0.133	0.169	−0.119	0.179			0	0.975
	2	0.507	0.003					−0.197	0.050					1.581	0.962
	3	0.729	<0.001											4.205	0.925
SCR [j]	1	0.449	0.009			0.168	0.077					0.081	0.116	0	0.920
	2	0.242	0.371			0.160	0.106			−0.115	0.391			0.131	0.935
	3					0.169	0.078			−0.222	0.009	0.062	0.216	0.029	0.918
	4					0.189	0.059			−0.237	0.006			1.033	0.886
	5									−0.308	0.002			3.761	0.783
NCY [k]	1	0.307	0.016			0.047	0.193	0.124	0.101			0.072	0.020	0	0.902
	2	0.336	0.011			0.134	0.093					0.076	0.018	1.731	0.857
	3	0.182	0.017									0.062	0.052	3.076	0.763

[a]DV: Dependent variable
[b]R^2: (Null Deviance - Residual Deviance)/(Null Deviance)
[c]GH: Grey Heron (*Ardea cinerea*)
[d]GE: Great Egret (*A. alba*)
[e]IE: Intermediate Egret (*Egretta intermedia*)
[f]LE: Little Egret (*E. garzetta*)
[g]ECE: Eastern Cattle Egret (*Bubulcus coromandus*)
[h]BNH: Black-crowned Night Heron (*Nycticorax nycticorax*)
[i]CS: colony size
[j]SCR: species composition ratio
[k]NCY: number of consecutive years

Table 3 Model results examining the effects of the existence of and changes in Grey Herons (*Ardea cinerea*) on the persistence period of the colonies using the data from 1997 to 2012

AIC	R^2	Explanatory variables		
		GH exist	GH change	GH exist × GH change
Cox proportional hazard model				
81.379	0.441	**-1.983***	-141.6	
83.375	0.441	**-1.987***	119.5	-1083.0
85.848	0.324		-171.7	
109.45	0.388	**-3.914****		
Parametric model				
140.18	0.575	17.74	3003.02	
142.18	0.575	17.74	3767.00	-3291.58
143.64	0.501		3767.69	
179.87	0.445	**48.67*****		

Values for the explanatory variables indicate coefficients fitted by the respective models. Bold values indicate the significant variables (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). GH exist: mean proportion of Grey Heron existence, which is from a binary variable (0: absent, 1: existing) of species composition data for each year, during the persistence period of the colony; GH change: an index of changes in Grey Heron existence during the persistence period of the colony, which is from the coefficient of a simple linear regression between Grey Heron existence (binary variable) and the persistence period of each year weighted by R^2; GH exist × GH change: interaction of GH exist and GH change.

Table 4 Model results examining the effects of the mean colony size and the proportion of each constituent species on the persistence period of the colonies using the population census data from 2002 to 2012

AIC	R^2	Explanatory variables						
		GH	GE	IE	LE	ECE	BNH	CS
Cox proportional hazard model								
35.188	0.705					**38.77****	**-11.89***	**-0.008***
36.684	0.710				6.206	**36.94****	**-11.24***	**-0.008***
37.005	0.707		9.172			**40.05****	**-12.74***	**-0.009***
37.116	0.705			1.409		**38.06****	**-11.82***	**-0.009***
37.160	0.705	-0.628				**37.86****	-12.62	**-0.009***
Parametric model								
62.252	0.736					**-51.4*****	**13.5****	**0.009*****
63.962	0.739			-4.155		**-50.152*****	**14.116****	**0.011****
64.122	0.737				-4.155	**-49.521*****	**13.034****	**0.010*****
64.219	0.736		5.05			**-51.1*****	**13.2****	**0.010****
64.238	0.736	0.684				**-50.485*****	14.409	**0.010***

Values for the explanatory variables indicate coefficients fitted by the respective models. Bold values indicate the significant variables (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). GH: Grey Heron; GE: Great Egret (*Ardea alba*); IE: Intermediate Egret (*Egretta intermedia*); LE: Little Egret (*E. garzetta*); ECE: Eastern Cattle Egret (*Bubulcus coromandus*); BNH: Black-crowned Night Heron (*Nycticorax nycticorax*); CS: colony size, which represents the total number of individual herons and egrets (except Black-crowned Night Herons) in the colony estimated by aerial photographic counts using a small radio-controlled paraglider (Chapter 1).

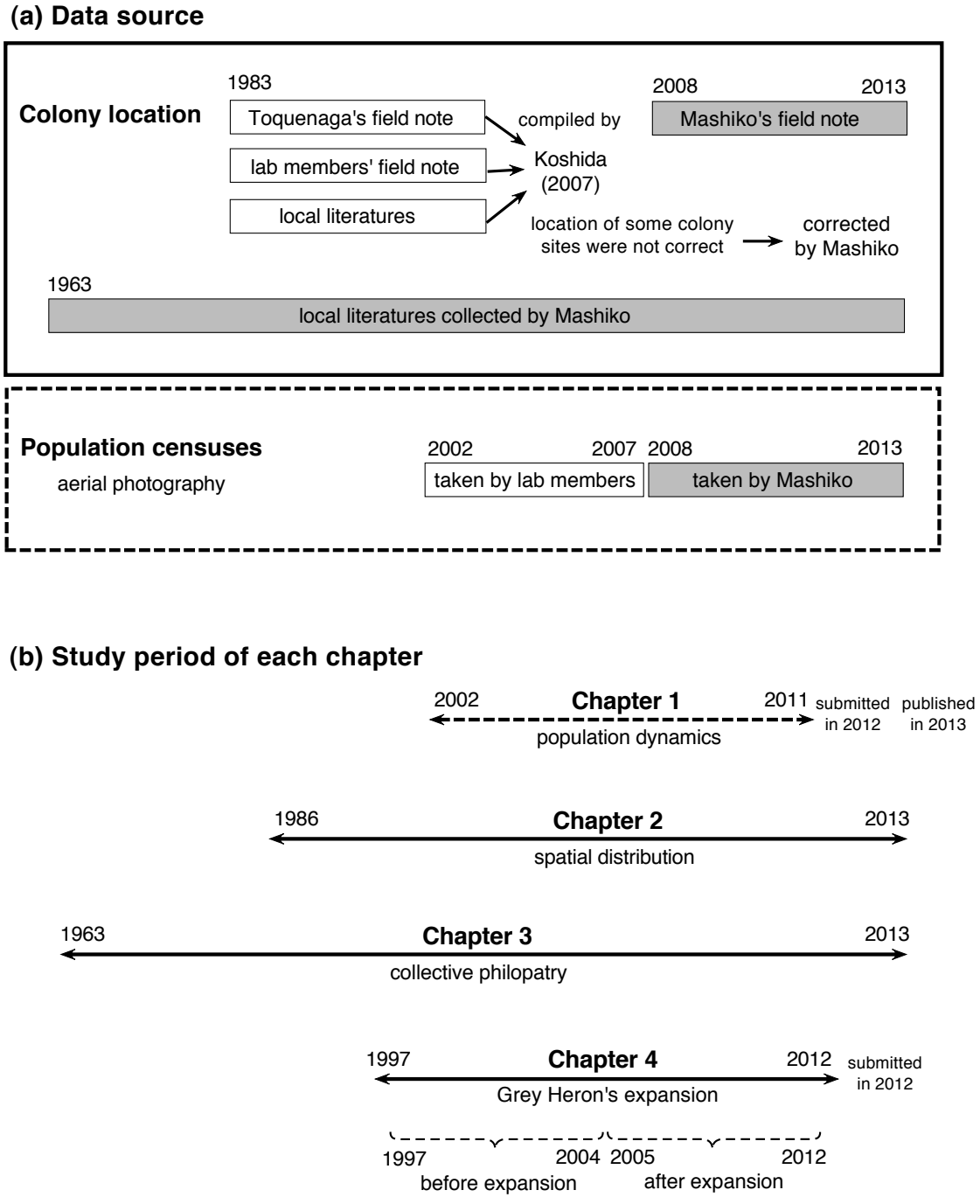

Figure 1 (a) Data sources and (b) study period of each chapter in this study. Study period was set so as to suit the theme of each chapter. Data obtained from population censuses (broken lines) were used in Chapter 1 and partially used in Chapter 4 for identifying the existence of Grey Herons. Chapter 2 and 3 used the colony-location data (bold lines) only. Note that the study period of Chapter 1 and 4 ended before submission of the manuscript.

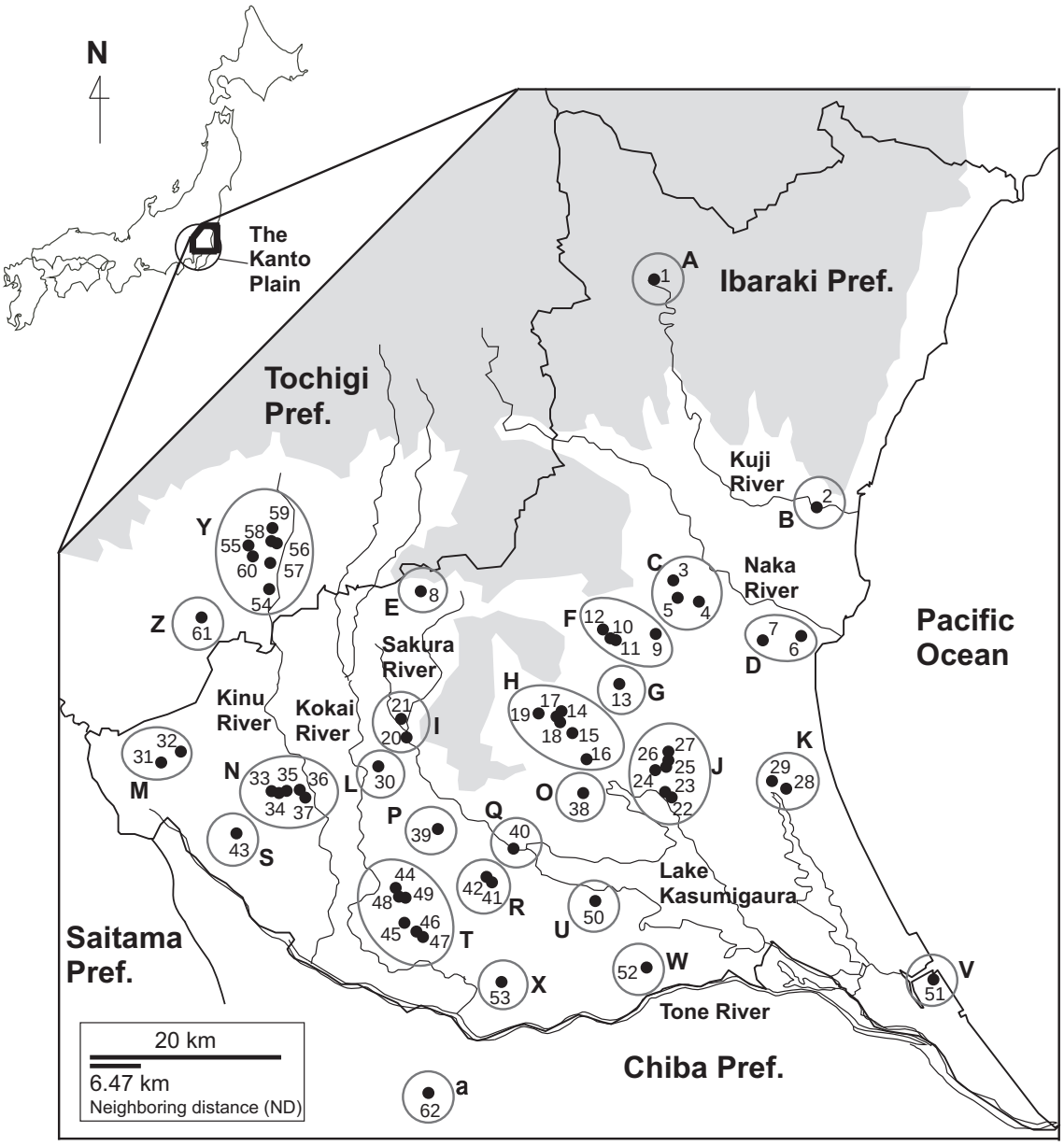

Figure 2 Locations of colonies from 2002 to 2011. Gray regions show an altitude greater than 100 m where the distribution of egrets is lower. Dots enclosed by a circle are considered to be historically identical colonies. Exceptionally, there are two cases in which the nearest-neighbor distance is shorter than 6.47 km; (1) $\mathbf{I}_{20}$ - $\mathbf{L}_{30}$: because **L** was newly established in 2010 and consisted of Grey Herons *Ardea cinerea* and Great Cormorants *Phalacrocorax carbo*, I assumed **L** was different from **I**. (2) $\mathbf{Q}_{40}$ - $\mathbf{R}_{41,42}$: **Q** was newly established in 2006, whereas Koshida (2007) reported that **R** has existed since 1984. It is difficult to assume that **Q** and **R** are one colony.

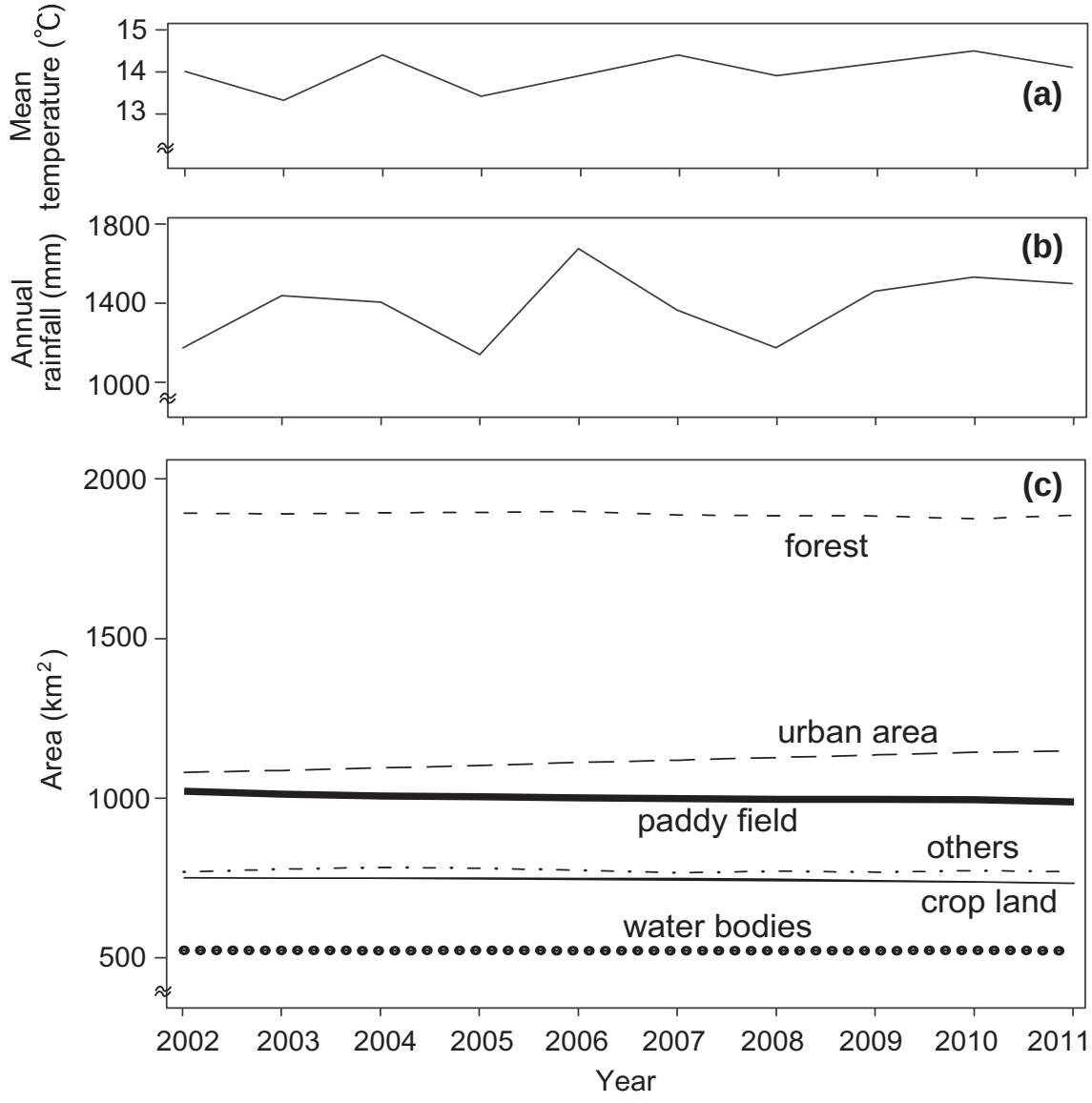

Figure 3 Changes in (a) mean temperature, (b) annual rainfall, and (c) areas of six land-use types from 2002 to 2011 in Ibaraki Prefecture, which was the main region of the study area (6,096 km^2). 'Paddy field' includes both rice paddies and lotus fields, and 'others' includes parks, golf courses, and uncultivated fields. Data were downloaded 8 June 2013 from http://www.data.jma.go.jp/obd/stats/etrn/index.php for climate and http://www.pref.ibaraki.jp/bukyoku/kikaku/mizuto/ibarakinotochi/25/ibarakinotochi.htm for land use.

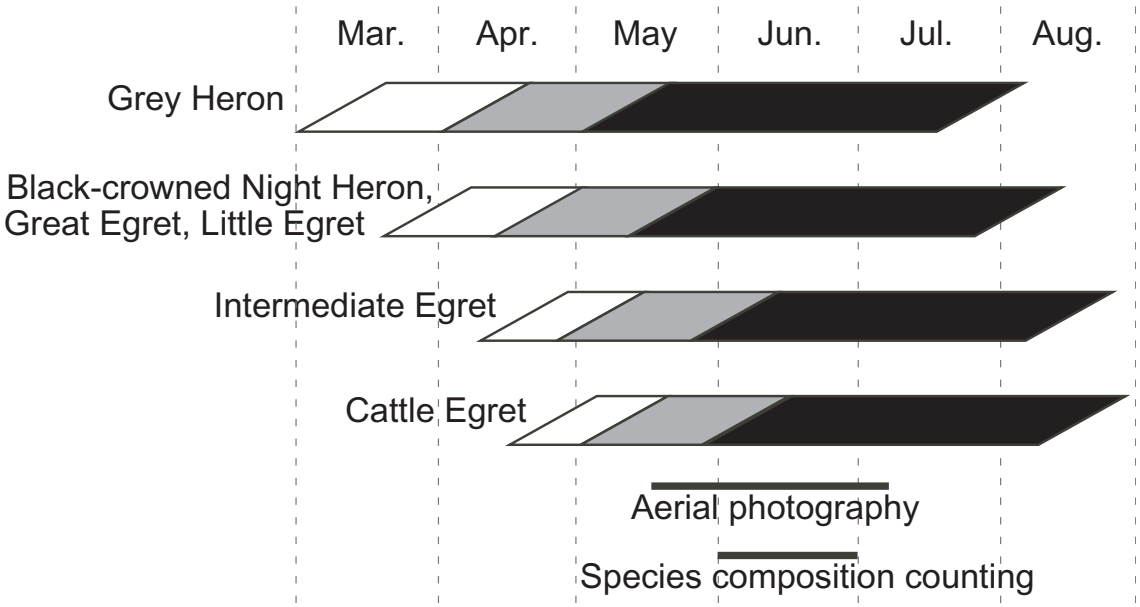

Figure 4 Breeding period of each species in the study area showing the timetable of aerial surveying and species composition counts. White, grey, and black shading show arrival and nest building, incubation, and chick-rearing periods, respectively. The parallelogram shapes indicate the variation in individual breeding periods. After breeding is over, some birds continue to roost in the colony but all disperse by October.

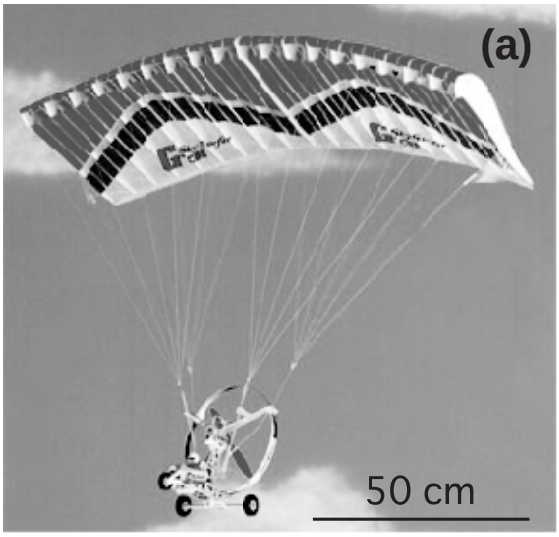

Figure 5 (a) Sky Surfer in flight (provided by Green Corporation), (b) An example of aerial photographs that show one part of a composite photograph (taken by M. Mashiko).

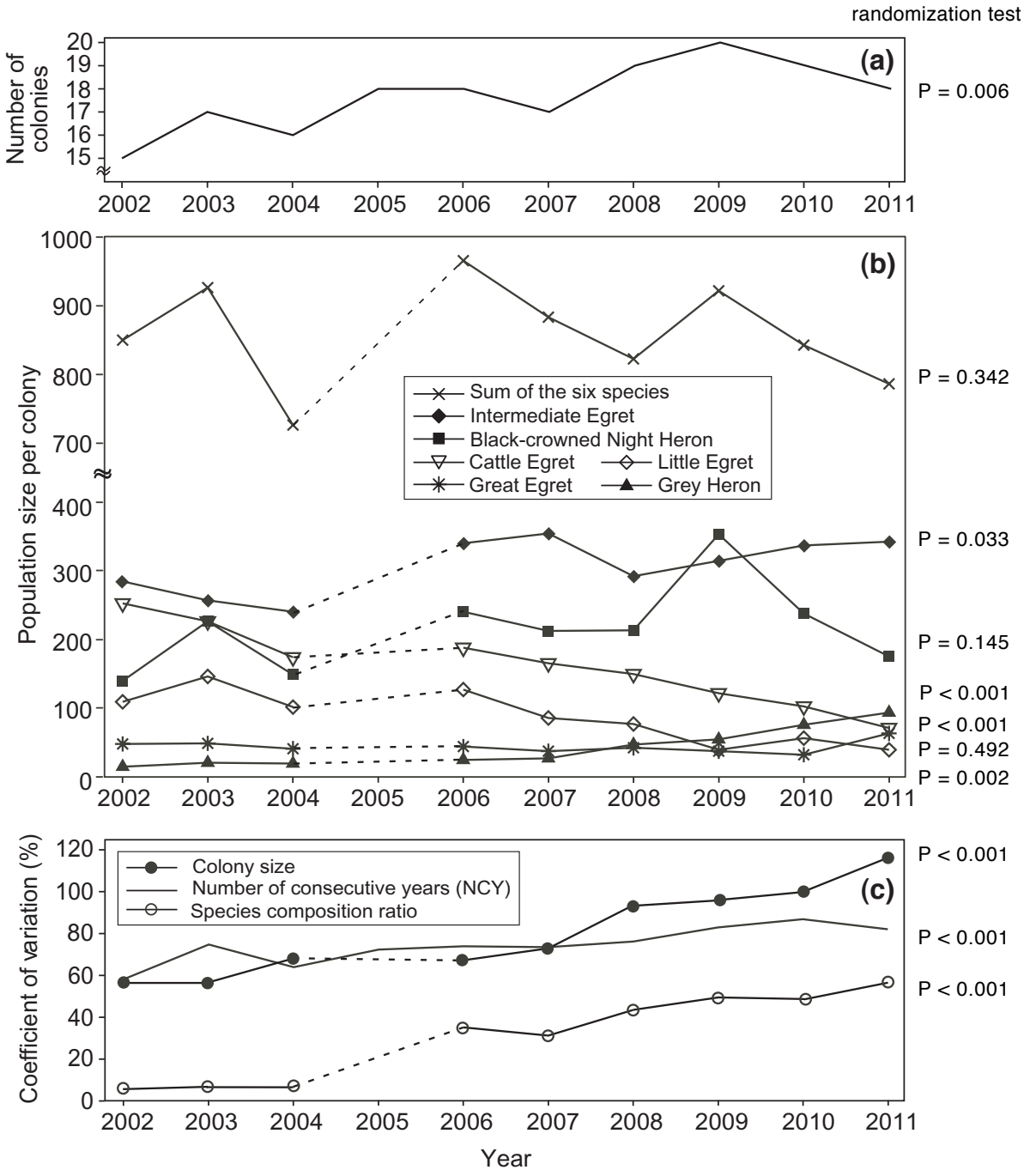

Figure 6 (a) Changes in the number of colonies between 2002 and 2011. (b) Changes in population per colony of each species and the sum of the six species. (c) Changes in the coefficient of variation (CV) of colony sizes, number of consecutive years (NCY), and species composition ratios. For the changes in population size and CVs of colony sizes and species composition ratios, the year 2005 is not shown because aerial and ground surveys were limited to only 5 out of 18 colonies.

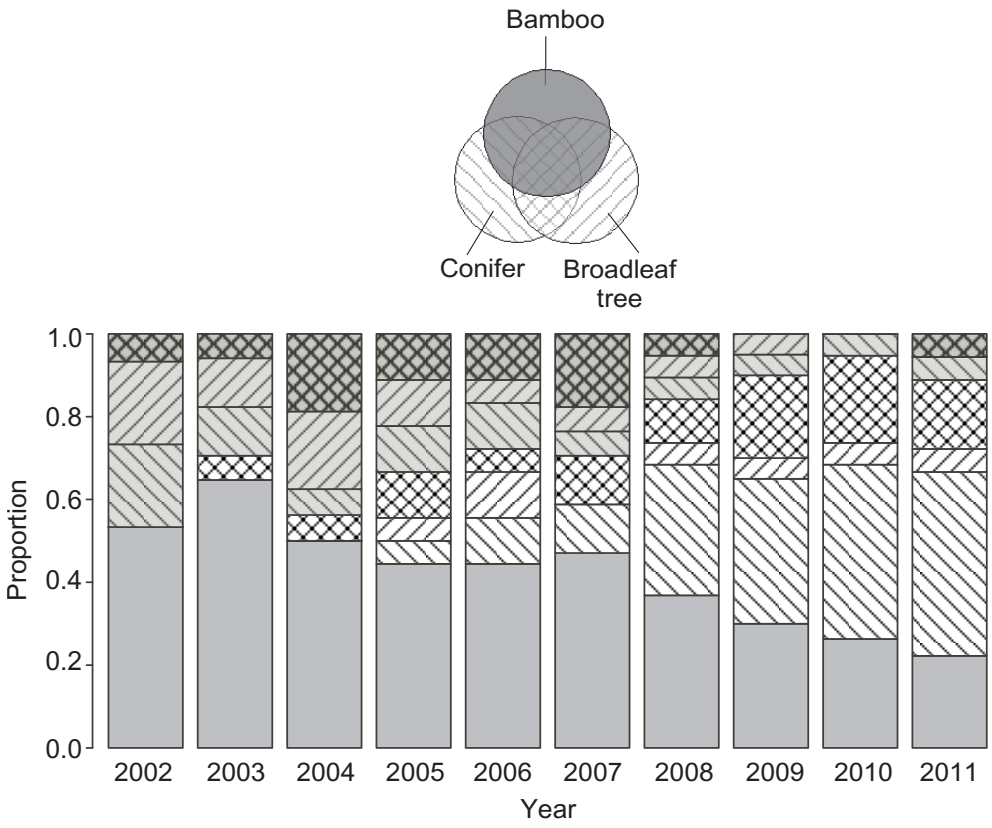

Figure 7 Changes in colony vegetation. See description of study area for details of species.

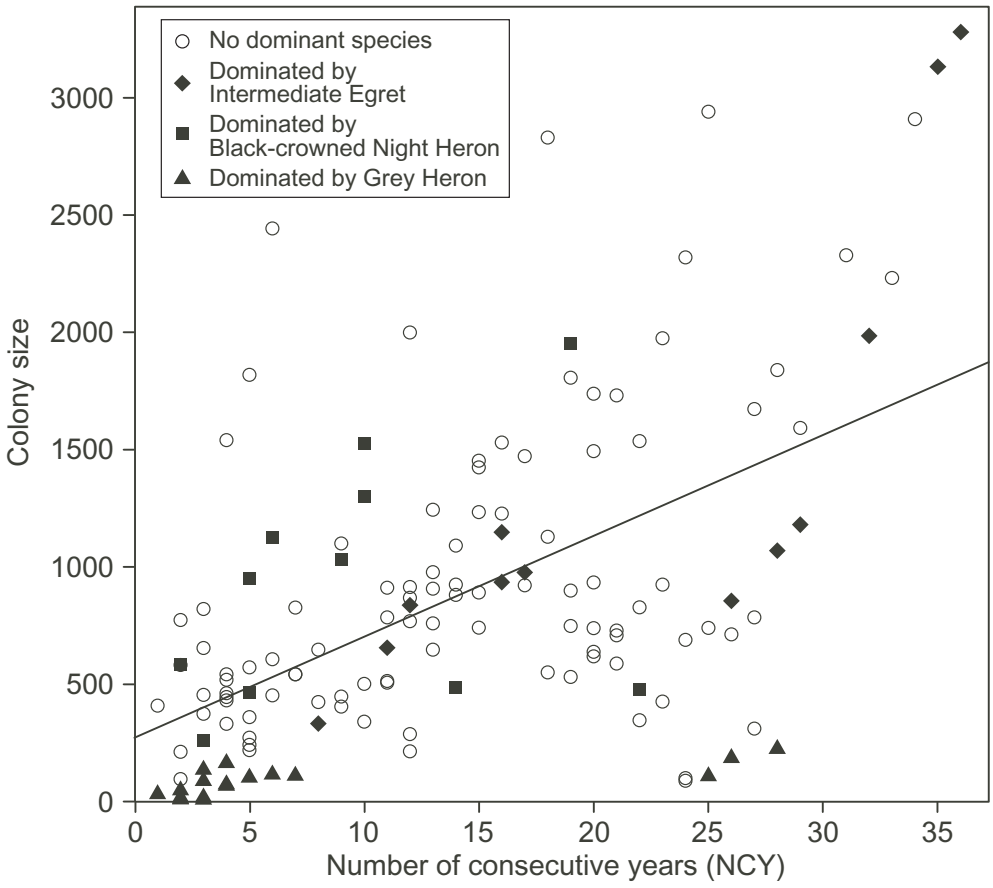

Figure 8 Relationship between colony size and longevity. Each dot represents a colony censused in a particular year ($n = 141$). The regression line was obtained by a linear regression analysis of colony sizes against longevity assuming that each annual colony was established independently.

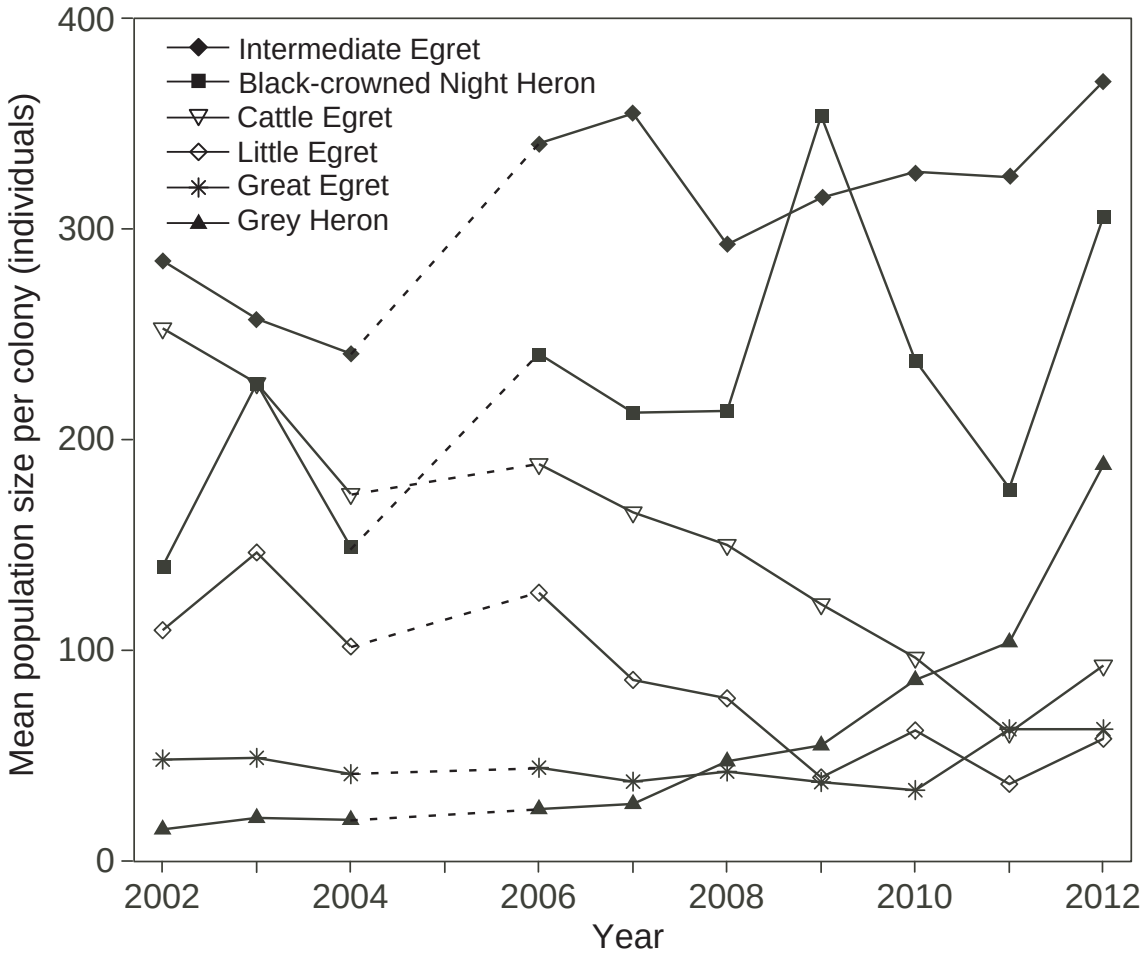

Figure 9 Changes in mean population size per colony of six species of herons and egrets in the study area from 2002 to 2012. The year 2005 is not shown because the population censuses based on a combination of aerial and ground surveys were limited to only 5 out of 18 colonies. For the other years, the percentage of censused colonies ranged from 78 to 94%. To avoid inappropriateness of using the simple sum of population size that is an increasing function of the number of colonies with census data, the population of each species was calculated annually using the mean population size per colony.

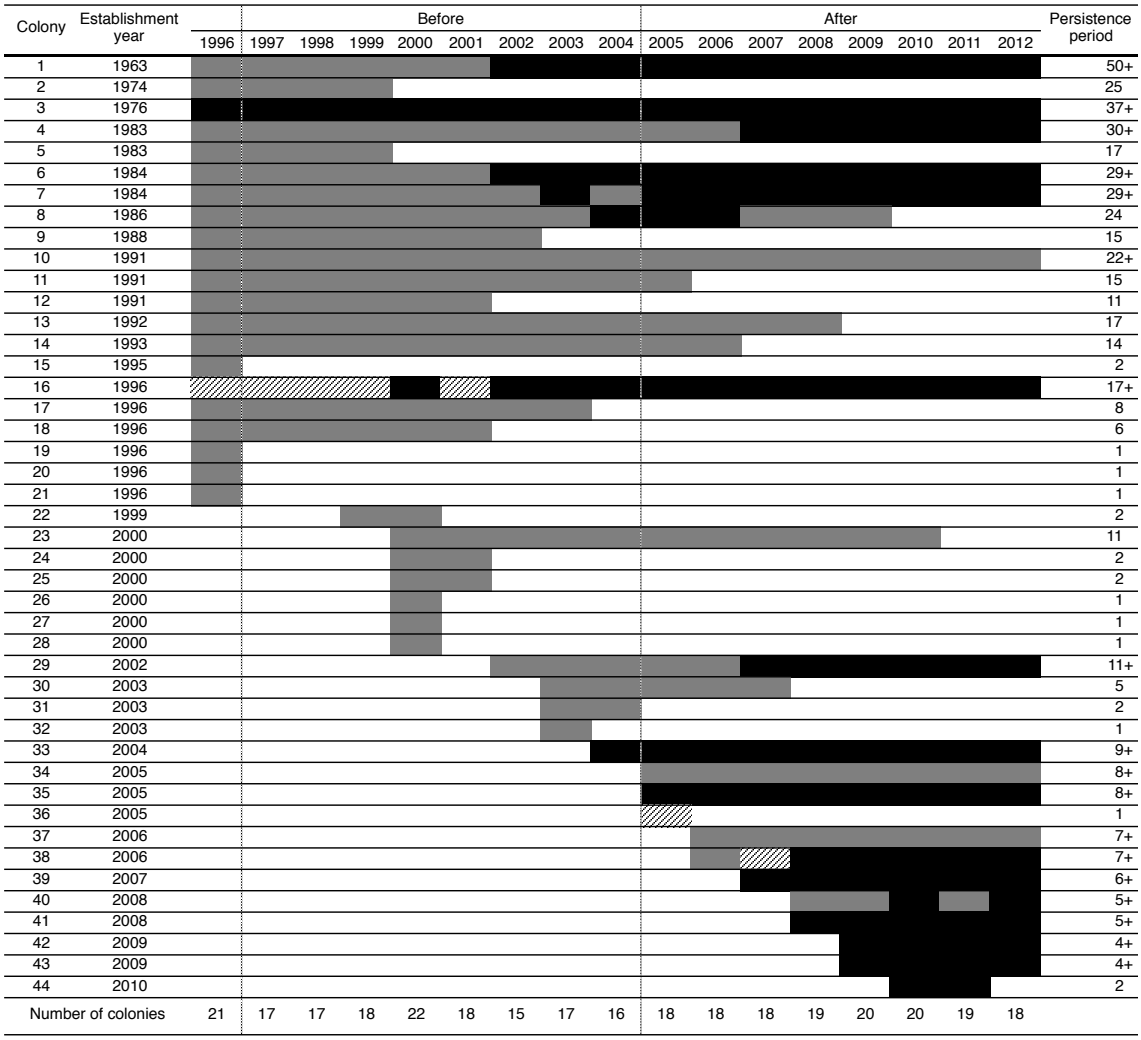

Figure 10 Establishment year, binary-state species composition, and the persistence period of 44 observed colonies from 1996 to 2012. Grey bars show the colonies without Grey Herons (*Ardea cinerea*), black bars show the colonies with Grey Herons, and hatched bars show the colonies for which binary-state species composition data was not available because of the shortage of observation records. "+" in the persistence period represents censored observation, i.e., an abandonment event was not observed before the end of my study period. Colonies in 1996 were only used for counting the number of abandoned colonies in 1997.

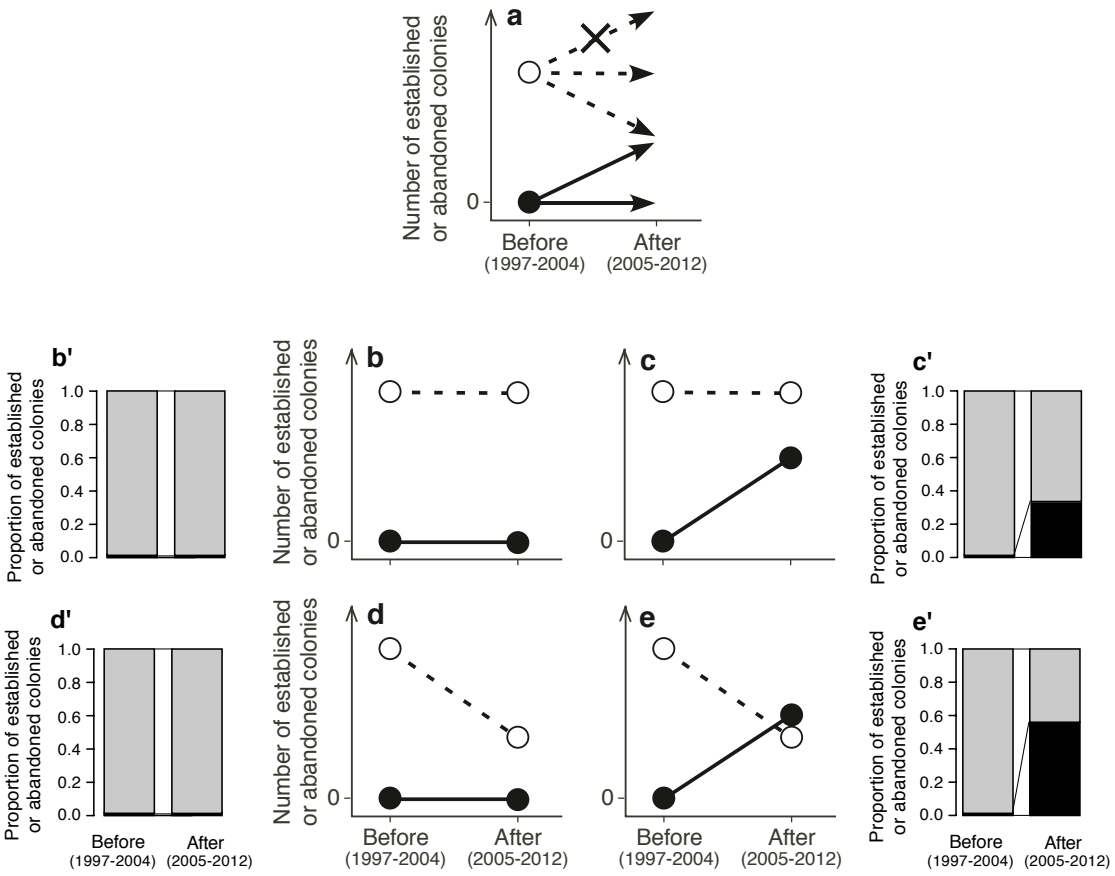

Figure 11 (a) Four possible patterns for the changes in the number of establishment and abandonment events before and after the expansion of Grey Herons and (b-e) four possible combinations of those changing patterns. Open circles with dashed lines represent the colonies without Grey Herons, and filled circles with solid lines represent the colonies with Grey Herons. (b'-e') show proportion of each combination. Grey and black bars correspond to open and filled circles, respectively.

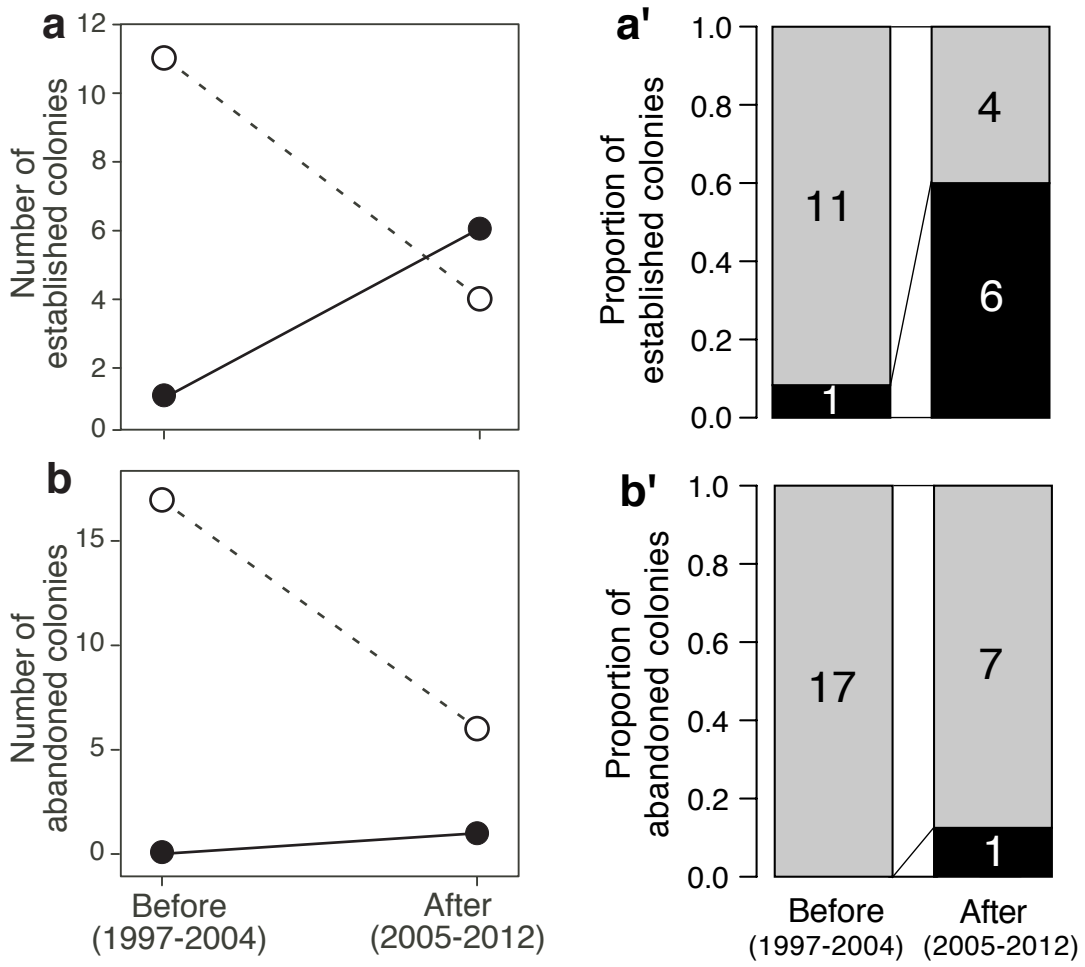

Figure 12 Number of (a) establishments and (b) abandonments of colonies before and after the expansion of Grey Herons. (a) Open circles with a dashed line represent the colonies without Grey Herons, and filled circles with a solid line represent the colonies with Grey Herons in the establishment year. (b) Open circles with a dashed line represent colonies that Grey Herons never joined during the persistence period (Grey Heron nonexistent: N). Filled circles with a solid line represent two categories: Grey Herons existed throughout the persistence period (Grey Heron throughout: T), and Grey Herons had existed but disappeared (Grey Heron disappeared: D). Since these two categories exhibited the same increasing pattern, these two lines are completely overlaid. (a') and (b') show proportion of established and abandoned colonies, respectively. Numbers in the bars represent the number of established or abandoned colonies. Grey and black bars correspond to open and filled circles, respectively.

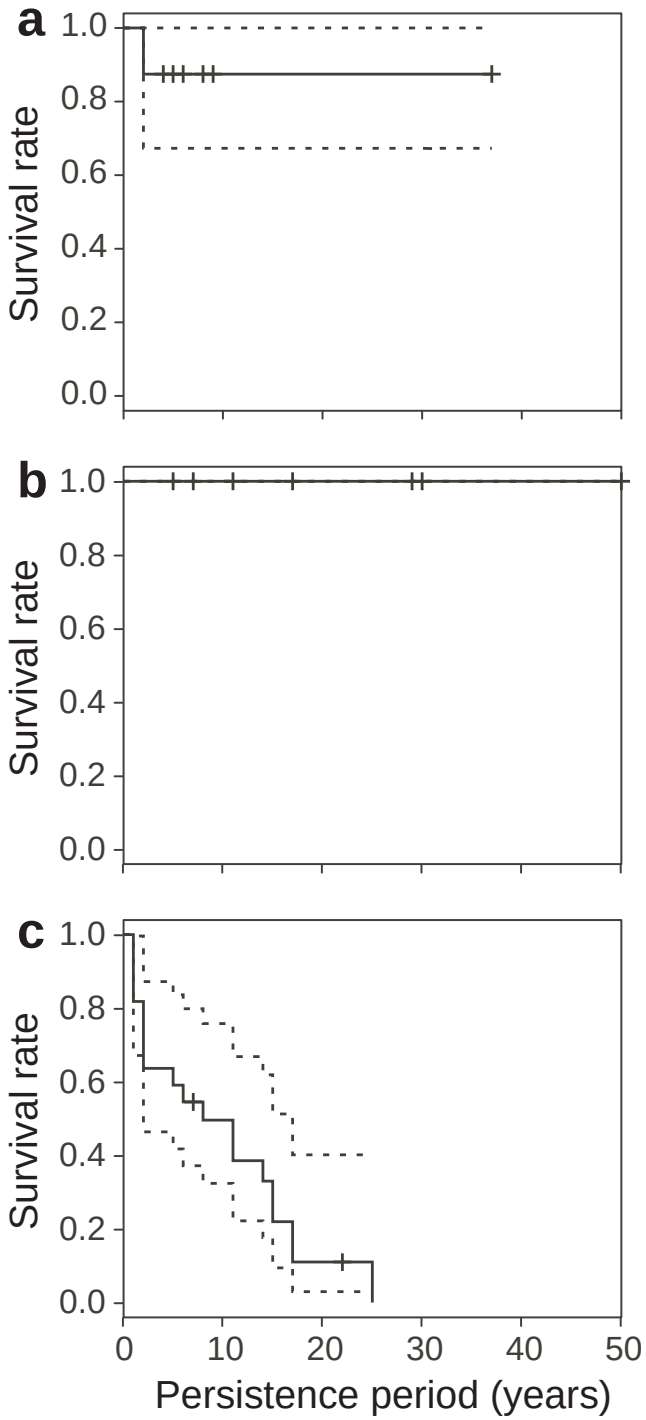

Figure 13 Survival curves for three patterns of the existence of *A. cinerea* during the persistence period of colonies using the Kaplan-Meier estimate with 95% confidence interval. (a) *A. cinerea* existed throughout the persistence period (Grey Heron throughout: T, $n = 8$), (b) *A. cinerea* joined already existing colonies (Grey Heron post-establishment: P, $n = 8$), and (c) *A. cinerea* never joined (Grey Heron nonexistent: N, $n = 22$). Vertical bars represent the censored observations.

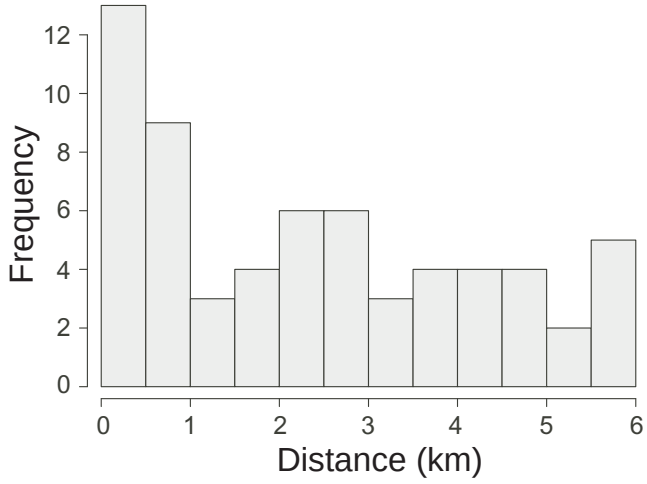

Figure 14 Histogram of displacement distances when colony-site shift was recorded during the study period from 1997 to 2012 ($n = 63$).

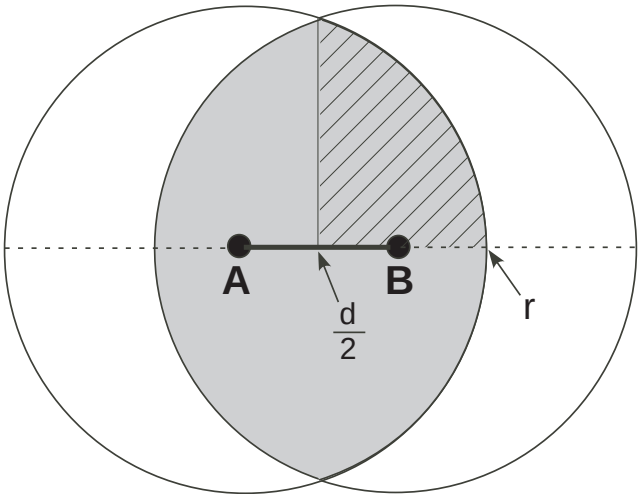

Figure 15 An image which shows the overlap of foraging range between an abandoned colony site (A) and a newly established colony site (B) when their displacement distance (d, bold line) is 6.39 km and the foraging range (r, solid line) has a radius of 10 km from each colony site.